Explorando el efecto de los usos del suelo sobre la biodiversidad y los servicios de los ecosistemas: un análisis basado en la diversidad taxonómica y funcional

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Explorando el efecto de los usos del suelo sobre la biodiversidad y los servicios de los ecosistemas: un análisis basado en la diversidad taxonómica y funcional

Memoria presentada por Violeta Hevia Martín para optar al Grado de Doctora en Ecología por la Universidad Autónoma de Madrid

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A mi abuelo, mi primer y mejor maestro

A mi abuela, mi guerrera favorita

In memoriam

“La ciencia es bella, y es por esa belleza que debemos trabajar en ella”.

Marie Curie

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Summary

In the context of Global Change, biodiversity loss is severely affecting ecosystem functioning and the delivery of ecosystem services, with important repercussions on human well-being. Ecosystems are exposed to several direct drivers of change, among which land use change stands out as the main direct cause of biodiversity degradation and erosion at a global scale. Land use changes have been particularly relevant in the rural areas of Mediterranean Europe, where they have been mainly dominated by two opposing processes: i) intensification of the most productive areas, and ii) abandonment of the most marginal areas. In particular, agricultural intensification is currently one of the human activities that is having major negative effects on biodiversity and the provision of ecosystem services.

This PhD dissertation aims to contribute to the general understanding of the effects of direct drivers of change on taxonomic and functional diversity in several groups of organisms, and the implications on the provision of ecosystem services. For this purpose, this research uses the conceptual framework of "response and effect" functional traits, which is a very useful and widely recognized approach for exploring the relationships between the direct drivers of change and ecosystem services. To achieve the specific objectives, we compiled and systematized existing evidence on some of these relationships. Furthermore, we conducted three case studies in the Cañada Real Conquense (Castilla-La Mancha, Spain) and Sierra Morena Oriental (Andalusia, Spain) to expand current knowledge on the functioning, direction, and intensity of links among the direct drivers of change, biodiversity, and ecosystem services.

The Results of this PhD dissertation are structured into four main sections. In the first section, a systematic review and meta-analysis is performed to synthesize existing empirical evidence on the relationships between the direct drivers of change and ecosystem services mediated by functional traits in three groups of organisms (vegetation, invertebrates, and vertebrates). The results of this review show: i) important gaps and biases in published studies; ii) evidence on the relationships between direct drivers of change and regulation services mediated by functional traits of vegetation and invertebrates; and iii) the existence of potential "key functional traits" that respond to the direct drivers of change and, simultaneously, have the capacity to influence the

provision of ecosystem services, being also relatively easy to measure and relevant to a wide range of organisms.

In the second section, we explore the effect of land use intensification on the taxonomic and functional diversity of several groups of organisms through a case study in Sierra Morena Oriental. The results show that taxonomic and functional diversity do not respond in the same way to intensification, following different trajectories that widely vary depending on the biotic group studied and the spatial scale of analysis.

In the third and fourth sections, we analyze the effect of livestock drove roads on the assemblages of ants and bees. The results show higher values of ant and bee diversity on the drove road, with a positive influence in the adjacent croplands. Furthermore, we evaluate how the bee assemblages of the Cañada Real Conquense affect pollination services and agricultural production in adjacent sunflower crops. The results show that the drove road acts as a reservoir of wild bee diversity, enhancing wild bee visitation to sunflower heads, increasing seed set.

Finally, the general Discussion of the Thesis addresses three fundamental questions. First, the role of land use intensification and its effects on biodiversity and the provision of ecosystem services, identifying the factors that contribute to the multifunctionality of Mediterranean agroecosystems. Second, the advantages and disadvantages of using the framework based on "response and effect" functional traits to develop general predictive rules on the effects of Global Change on biological communities, particularly regarding the role of functional redundancy and its relationships with ecosystem resilience. Finally, the limitations in using functional traits as a methodological and conceptual approach, proposing future challenges for research in this field.

Resumen

En el actual contexto de Cambio Global, la pérdida de biodiversidad está afectando de forma severa al funcionamiento de los ecosistemas y al suministro de los servicios que éstos generan, con importantes repercusiones sobre el bienestar humano. Los ecosistemas están expuestos a diferentes impulsores directos de cambio, entre los cuales, el cambio de uso del suelo destaca como la principal causa directa de la degradación y pérdida de biodiversidad a nivel global. Los cambios de uso del suelo han sido particularmente relevantes en las zonas rurales de la Europa Mediterránea, donde han estado dominados principalmente por dos procesos contrapuestos: la intensificación en las áreas más productivas y el abandono de tierras en las zonas más marginales. La intensificación de la agricultura, en concreto, se presenta actualmente como una de las actividades antrópicas que afecta más negativamente a la biodiversidad y al suministro de servicios de los ecosistemas.

El objetivo general de la Tesis Doctoral es contribuir a la comprensión de los efectos de los impulsores directos de cambio sobre la diversidad (taxonómica y funcional) de distintos grupos de organismos, y su traducción en el suministro de servicios de los ecosistemas. Para ello, en esta investigación se utiliza el marco conceptual basado en los rasgos funcionales de "respuesta y efecto", por ser una aproximación muy útil y ampliamente reconocida para explorar las relaciones entre los impulsores directos de cambio y los servicios de los ecosistemas. Para la consecución de los objetivos específicos de la Tesis, se han recopilado y sistematizado las evidencias existentes acerca de algunas de estas relaciones, y se han desarrollado tres casos de estudio en la Cañada Real Conquense y Sierra Morena Oriental, que permiten comprender mejor el funcionamiento, dirección e intensidad de los vínculos entre impulsores directos de cambio, biodiversidad y servicios de los ecosistemas.

Los resultados de la Tesis se estructuran en cuatro grandes apartados. En el primero de ellos, se realiza una revisión sistemática de la literatura y un meta-análisis para sintetizar la evidencia empírica existente sobre las relaciones entre los impulsores directos de cambio y los servicios de los ecosistemas mediadas por rasgos funcionales en tres grupos de organismos (vegetación, invertebrados y vertebrados). Los resultados de dicha revisión muestran i) la existencia de importantes vacíos de información y sesgos en las investigaciones realizadas hasta la fecha en este campo; ii) la existencia de

evidencias sobre las relaciones entre los cambios de uso del suelo y diversos servicios de regulación, mediadas por rasgos funcionales de plantas e invertebrados; y iii) la existencia de potenciales "rasgos funcionales clave" que responden a los impulsores directos de cambio y tienen simultáneamente un efecto sobre los servicios de los ecosistemas, siendo además relativamente fáciles de medir y relevantes en un rango amplio de tipos de organismos.

En el segundo apartado, se explora a través de un caso de estudio en Sierra Morena Oriental, el efecto de la intensificación en el uso del suelo sobre la diversidad taxonómica y funcional de varios grupos de organismos. Los resultados muestran que la diversidad taxonómica y la diversidad funcional no responden de la misma forma frente a la intensificación, sino que siguen trayectorias diferentes que varían, en gran medida, en función del grupo biótico estudiado y de la escala espacial analizada.

En los apartados tercero y cuarto de Resultados, se analiza el efecto de las vías pecuarias con uso ganadero sobre las comunidades de hormigas y abejas, detectándose un efecto positivo sobre los valores de diversidad de ambos grupos, tanto en las propias vías pecuarias como los campos de cultivo colindantes presentes en las zonas de estudio. Además, se evalúa el efecto de la comunidad de abejas silvestres presente en la Cañada Real Conquense sobre el servicio de polinización y la producción agrícola en los campos intensivos de girasol adyacentes a dicha vía pecuaria, encontrándose que ésta no sólo actúa como reservorio de la diversidad de abejas silvestres, sino que favorece un mayor número de visitas de las abejas silvestres a los girasoles, aumentando también la producción de semillas.

Finalmente, la discusión general de la Tesis se articula alrededor de tres cuestiones fundamentales: i) el papel de la intensificación de los usos del suelo y sus efectos sobre la biodiversidad y el suministro de servicios de los ecosistemas, identificando los factores que contribuyen a una mayor o menor multifuncionalidad de los agroecosistemas mediterráneos; ii) las ventajas e inconvenientes del uso del marco basado en los rasgos funcionales de "respuesta y efecto" para el desarrollo de reglas predictivas generales sobre los efectos del Cambio Global en las comunidades biológicas, discutiendo el papel de la redundancia funcional y sus relaciones con la resiliencia de los ecosistemas; y por último iii) las limitaciones identificadas en el uso de los rasgos funcionales como aproximación metodológica y conceptual, así como la propuesta de nuevos retos futuros para la investigación en este campo.

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Capítulo 1

Introducción

1.1 El Cambio Global como contexto

Vivimos tiempos de cambios sin precedentes en la historia de la humanidad, que se traducen en una crisis global definida por los desequilibrios y perturbaciones que afectan al funcionamiento de los ecosistemas a todas las escalas. La mayor parte de estos cambios son generados y/o están acelerados por las actividades humanas (Schröter et al. 2005). En este sentido, se ha denominado **Cambio Global** al conjunto de cambios ambientales producidos por la actividad del ser humano que afectan al funcionamiento del sistema Tierra a una escala global (Jiménez-Herrero et al. 2011).

Si bien es cierto que existen múltiples aproximaciones en cuanto a la identificación de sus componentes, los efectos de este Cambio Global son visibles principalmente a través de la crisis demográfica, energética, de alimentos, o medioambiental (Duarte et al. 2006). El Cambio Global, por tanto, no puede ser entendido como un fenómeno simple de causa-efecto, ya que los cambios ambientales que lo ocasionan tienen efectos múltiples, a diferentes escalas (espaciales y temporales), y con un gran número de interacciones que son además difíciles de identificar y predecir.

A pesar de las múltiples peticiones de acción (MA 2005; TEEB 2010) y metas acordadas en diferentes iniciativas internacionales (Cumbre de las Naciones Unidas sobre el Desarrollo Sostenible "Rio+20" 2012; Cumbre del clima de París 2015), los ecosistemas continúan estando expuestos a fuertes presiones (Butchart et al. 2010). Desde los años 70, las demandas de bienes y servicios de la población mundial han superado la capacidad del planeta para generarlos de una manera sostenible (Costanza 2000; Blomqvist et al. 2013). Precisamente para hacer frente a esas demandas, algunas actividades humanas son cada vez más invasivas y agresivas con los ecosistemas. La Evaluación de los Ecosistemas del Milenio puso de manifiesto que el ser humano ha transformado los ecosistemas en los últimos 60 años más rápidamente que en ningún otro periodo anterior en la historia de la humanidad (MA 2005). En otras palabras, el ritmo, magnitud y alcance de las alteraciones humanas sobre los ecosistemas de nuestro planeta no tiene precedentes (Lambin et al. 2001).

El Cambio Global, por tanto, se ha convertido en una realidad ineludible que se traduce en un desafío global (pero que afecta a todas las escalas espacio-temporales) que debemos afrontar también (o quizá sobre todo) desde la esfera científica.

Además, las consecuencias socioeconómicas del Cambio Global dependerán precisamente de cómo se traduzcan dichos cambios en alteraciones sobre los procesos y servicios de los ecosistemas (Costanza et al. 1997; Balmford et al. 2002; MA 2005). Por tanto, la ciencia se enfrenta a un enorme reto: la necesidad de predecir con la mayor precisión posible cómo responderán los ecosistemas a dichos cambios.

Las causas y consecuencias del Cambio Global nacen de una transformación en las relaciones entre los seres humanos como especie y los ecosistemas. Con el objetivo de darle una entidad propia a este complejo entramado de relaciones, hace poco más de una década se propuso y definió el "**Antropoceno**" como una nueva era geológica (Crutzen y Stoermer 2000). La propuesta de esta nueva era se sustenta sobre dos argumentos clave: i) que las dinámicas del Sistema Tierra se están alejando de aquellas que caracterizan a la época geológica actual (Holoceno); y ii) que la actividad humana se ha convertido en una fuerza geológica global en sí misma (Steffen et al. 2011).

Los esfuerzos destinados a la identificación y clasificación de las principales causas del Cambio Global llevaron a denominar lo que se conoce como "*impulsores del cambio*", y que fueron definidos por Carpenter y Folke (2006) como "cualquier factor natural o de origen antrópico que directa o indirectamente provoca un cambio en un ecosistema". Se pueden distinguir dos tipos de impulsores de cambio: i) **impulsores directos**, que son aquellos cuyo impacto repercute directamente sobre los procesos ecológicos (principalmente: cambios de uso del suelo, cambio climático, contaminación, introducción de especies invasoras, cambios sobre los ciclos biogeoquímicos, y sobre-explotación de los servicios de los ecosistemas); así como ii) **impulsores indirectos**, que son aquellos que alteran el funcionamiento de los ecosistemas por medio de su acción sobre uno o varios impulsores directos de cambio (principalmente: tendencias demográficas, sistema económico, tendencias sociopolíticas, tecnología, o factores culturales como los patrones de consumo, la identidad, los valores, etc.) (MA 2005).

Mientras que las perturbaciones naturales generan efectos relativamente discretos y son los motores de la dinámica de los ecosistemas, los impulsores de cambio se caracterizan por producir efectos aditivos y sinérgicos que resultan difícilmente predecibles (Sala et al. 2000). Además, los impulsores de cambio operan a múltiples escalas (Marty et al. 2014), y por lo tanto, los efectos que generan sobre los organismos y ecosistemas pueden llegar a ser sumamente complejos. Entre todos los impulsores de cambio identificados y descritos hasta la fecha, los **cambios de uso del suelo** destacan como la

principal causa directa de la degradación de ecosistemas y la pérdida de biodiversidad (Vitousek et al. 1997; Sala et al. 2000; Foley et al. 2005). Por ejemplo, más de dos tercios del área de dos de los mayores biomas terrestres ("matorrales y bosques mediterráneos" y "estepas y bosques templados"), y más de la mitad del área de otros cuatro grandes biomas han sido convertidos a otros usos de suelo (principalmente sistemas agrarios) durante el siglo XX (MA 2005; Fig. 1.1).

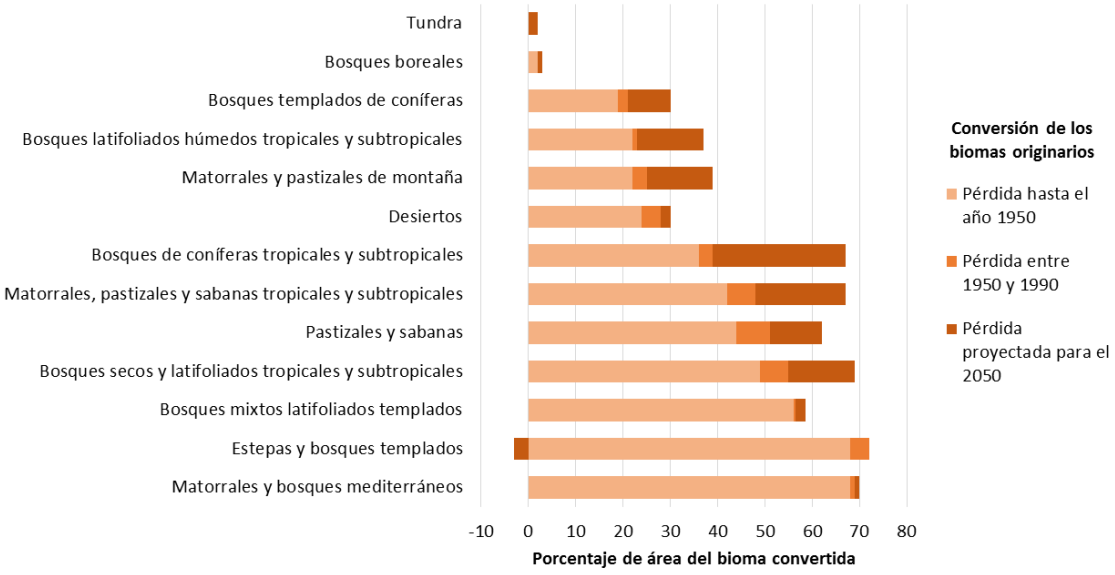

Figura 1.1 Porcentaje de área convertida de cada tipo originario de bioma **i)** hasta el año 1950, **ii)** entre 1950 y 1990, y **iii)** hasta 2050 según el escenario "*Orden desde la fuerza*" desarrollado por el MA (2005) para explorar futuros plausibles para los ecosistemas y el bienestar humano, basados en diferentes supuestos sobre las fuerzas impulsoras de cambio y sus posibles interacciones. La mayor parte de las conversiones detectadas son cambios hacia sistemas cultivados (Adaptado de MA 2005).

Rockström et al. (2009) propusieron el concepto de "límites planetarios", para referirse a los umbrales por encima de los cuales existe el riesgo de que las perturbaciones humanas desestabilicen las funciones de los ecosistemas a escala planetaria. El cambio de uso del suelo se ha identificado como uno de los nueve límites planetarios, situándose además en la "zona de incertidumbre", es decir, con riesgo de alcanzar el umbral de cambio que desencadenaría efectos ecológicos irreversibles a escala global (Steffen et al. 2015).

Los cambios de uso del suelo están fuertemente asociados con pérdidas de hábitat naturales o semi-naturales que a su vez son, en buena medida, responsables de la crisis global de biodiversidad (Brooks et al. 2002; Newbold et al. 2016). Los cambios de uso del suelo han sido particularmente relevantes en la Europa mediterránea en las últimas décadas (Falcucci et al. 2007). Poniendo el foco en los principales tipos de cambio de uso del suelo, y siguiendo las tendencias globales, se ha detectado que en Europa la mayor parte de dichos cambios están relacionados con algún tipo de actividad agrícola, y particularmente con la expansión de la agricultura intensiva (van Vliet et al. 2015). Concretamente en España, este tipo de cambios de uso del suelo constituye el impulsor directo más relevante respecto a los efectos negativos sobre la biodiversidad (Fig. 1.2).

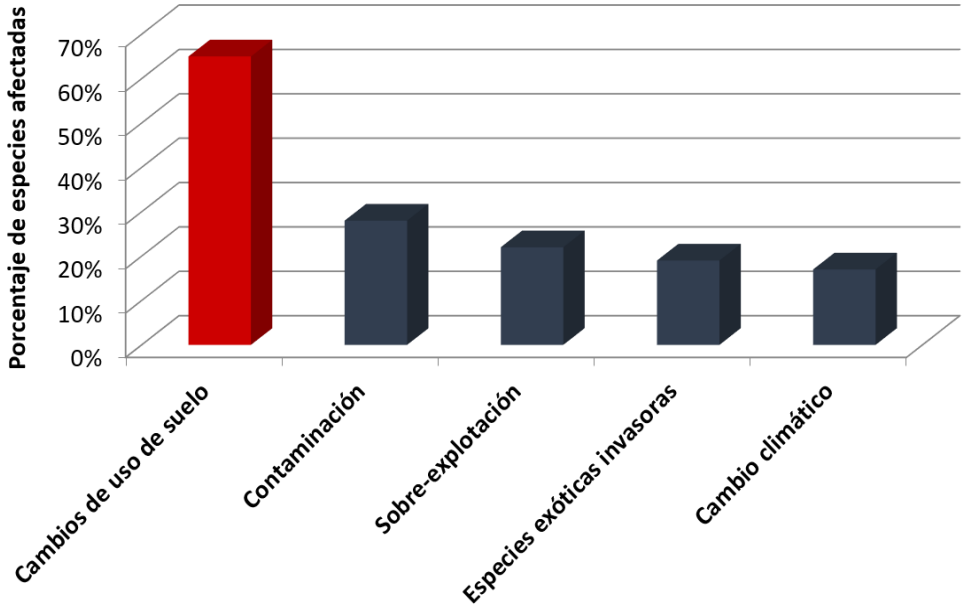

Figura 1.2 Principales impulsores directos de cambio que afectan a las especies catalogadas como amenazadas en España (Adaptado de EME 2011).

Dentro de los usos de suelo predominantes, es importante destacar el papel de los **agroecosistemas**, entendidos como "cualquier tipo de ecosistema modificado y gestionado por los seres humanos con el objetivo de obtener alimentos, fibras u otros materiales de origen biótico" (Gómez Sal 2001). A nivel global, los agroecosistemas ocupan en torno a un 38% de la superficie terrestre libre de hielo (Foley et al. 2011); mientras que en Europa la superficie ocupada por agroecosistemas se sitúa cerca del 45% (EASAC 2009); y en España asciende a cerca de un 60% (EME 2011).

Por todo esto, los cambios de uso del suelo en general, y los que tienen lugar en los agroecosistemas en particular, se erigen como uno de los impulsores directos más determinantes del Cambio Global. Una mayor comprensión de los efectos que tiene este impulsor de cambio sobre la biodiversidad y los ecosistemas puede ser determinante para predecir futuras consecuencias derivadas de algunas actividades humanas, principalmente relacionadas con la gestión y manejo del territorio.

1.2 Las Ciencias de la Sostenibilidad y los servicios de los ecosistemas como marco conceptual

En el contexto de Cambio Global, las formas de colaboración entre los científicos de diferentes disciplinas en busca de soluciones a los desafíos a los que nos enfrentamos, han hecho germinar nuevos paradigmas de pensamiento y conceptos como, por ejemplo: i) "los sistemas complejos" (Levin 1999); ii) "los sistemas socio-ecológicos" (Berkes y Folke 1998); y iii) la "resiliencia socio-ecológica" (Berkes y Folke 1998; Gunderson y Holling 2001), entre otros. Este florecimiento de nuevos cuerpos de conocimiento en los que confluyen las *Ciencias Biogeofísicas* y las *Ciencias Sociales* ha dado lugar a las **Ciencias de la Sostenibilidad** (Kates 2001). Esta disciplina emergente se constituye desde una aproximación multidisciplinar que persigue abordar las relaciones complejas existentes entre la naturaleza y la sociedad para dar un paso más en la comprensión de esta creciente inter-dependencia entre los sistemas naturales y sociales (Kates et al. 2001; 2011). Así, bajo el paraguas conceptual de las ciencias de la sostenibilidad, se plantean algunas cuestiones básicas que deben ser abordadas para avanzar en la investigación de las interacciones naturaleza-sociedad (Caja 1.1).

Caja 1.1 Cuestiones fundamentales que abordan las Ciencias de la Sostenibilidad (Propuesto por Kates et al. 2001)

- **¿Cómo pueden incorporarse mejor las interacciones dinámicas naturaleza-sociedad en modelos que integran el sistema Tierra, el desarrollo humano y la sostenibilidad?**
- **¿Cómo están reestructurando las interacciones naturaleza-sociedad la sostenibilidad de las tendencias ambientales y de desarrollo?**
- **¿Qué determina la vulnerabilidad o resiliencia de los sistemas naturaleza-sociedad en cada tipo de ecosistema y forma de vida?**
- **¿Pueden ser definidos los límites que sirvan de alerta para detectar las condiciones bajo las cuales un determinado sistema naturaleza-sociedad está en serio peligro de degradación?**
- **¿Qué sistemas (p.e. mercados, normas e información científica) pueden mejorar la capacidad social para guiar las interacciones entre la naturaleza y la sociedad hacia trayectorias más sostenibles?**
- **¿Cómo pueden integrarse los sistemas de monitoreo de las condiciones ambientales y sociales para proporcionar una guía más útil que permita la transición hacia la sostenibilidad?**
- **¿Cómo pueden integrarse mejor las actividades de investigación, monitoreo, evaluación, y de toma de decisiones en los sistemas de manejo y aprendizaje social?**

La Ecología desempeña un papel fundamental en la vertebración de esta nueva disciplina de cara a poder desarrollar visiones plausibles acerca de las relaciones entre las sociedades y los ecosistemas, a medio y largo plazo (Carpenter y Folke 2006).

En concreto, el marco de los **sistemas socio-ecológicos** (definidos como sistemas complejos adaptativos en los que interactúan los sistemas sociales y biofísicos) (Liu et al. 2007; Fig. 1.3) ha emergido con gran fuerza en los últimos años, siendo incorporado en varios programas internacionales de sostenibilidad (p.e. IPBES, Objetivos de Desarrollo Sostenibles de Naciones Unidas, etc.) (Fischer et al. 2015), y en diversas líneas de investigación orientadas a la conservación de la naturaleza (Mace 2014). A través de este marco común, y con el fin de comprender mejor el funcionamiento de los sistemas socio-ecológicos, es imprescindible un conocimiento profundo de las variables específicas que los determinan y de las interacciones entre las mismas (Ostrom 2009).

La pérdida de biodiversidad tiene efectos (directos o indirectos) sobre el bienestar humano, en tanto en cuanto compromete el funcionamiento de los ecosistemas y, por

tanto, su capacidad de generar servicios para la sociedad (Díaz et al. 2006; Mace et al. 2010; Rands et al. 2010). Sin embargo, durante la mayor parte del siglo XX, la conservación de la biodiversidad estuvo basada principalmente en criterios éticos que respondían al valor intrínseco de la propia biodiversidad (McCauley 2006). No fue hasta los años 70 que se empezaron a contemplar las funciones de los ecosistemas en términos de contribuciones para la sociedad, con el objetivo de aumentar el interés general en la conservación de la biodiversidad (de Groot 1987; Westman 1977). Concretamente, el término "servicios de los ecosistemas" fue introducido en la esfera científica a finales de los años 90 a través del libro titulado "Los servicios de la naturaleza: la dependencia de la sociedad de los servicios de los ecosistemas" (Daily, 1997). La Evaluación de los Ecosistemas del Milenio (MA 2003) se convirtió en una contribución esencial para situar los servicios de los ecosistemas en la agenda política, y desde entonces la literatura respecto a los servicios de los ecosistemas ha crecido de manera exponencial (Fisher et al. 2009). Actualmente, los servicios de los ecosistemas han sido definidos como "las contribuciones directas e indirectas de los ecosistemas al bienestar humano" (De Groot et al. 2010), o como "cualquier actividad o función de un ecosistema que suministra beneficios a los seres humanos (Mace et al. 2012) (ver Caja 1.2), y se clasifican en tres categorías (Martín-López et al. 2009):

- Los servicios de **abastecimiento**: aquellos productos obtenidos directamente de los ecosistemas (p.e. alimento, fibras vegetales, agua dulce, productos medicinales, madera, etc.).
- Los servicios de **regulación**: aquellas contribuciones obtenidas de los procesos de los ecosistemas y disfrutadas de un modo indirecto (p.e. polinización, control de plagas, depuración del agua, regulación del clima, etc.).
- Los servicios **culturales**: las contribuciones intangibles que las personas obtienen de los ecosistemas a través de experiencias (p.e. actividades recreativas, valor estético, sentido de identidad, etc.).

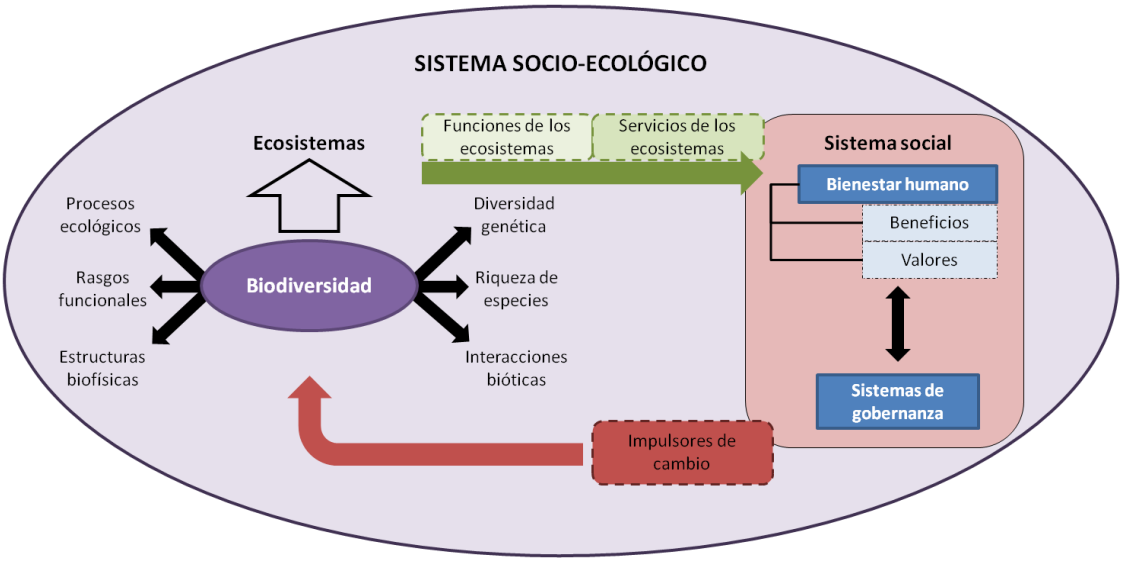

Figura 1.3 Esquema del marco conceptual de los sistemas socio-ecológicos (adaptado de Maes et al. 2013). Los distintos componentes de la biodiversidad desempeñan un papel clave en la estructura y funciones de los ecosistemas (parte izquierda del esquema). A su vez, éstos generan un flujo de servicios de los ecosistemas (flecha verde) que repercute en el bienestar de la población humana enmarcada en un sistema social (cuadro rosa). Los sistemas de gobernanza a través de las instituciones, actores sociales y usuarios de los servicios de los ecosistemas afectan a su vez a los ecosistemas por medio de los impulsores de cambio (flecha roja).

Uno de los principales retos de las Ciencias de la Sostenibilidad se centra en conocer y comprender los mecanismos que explican el potencial de los ecosistemas para suministrar servicios, así como explorar las sinergias entre diferentes servicios de los ecosistemas (Bennet et al. 2009; Lavorel y Grigulis 2012). De cara a contribuir a la elaboración de políticas que se traduzcan en mejores herramientas de gestión que permitan la conservación de los ecosistemas y, por tanto, el uso sostenible de los servicios de los ecosistemas, es imprescindible la comprensión ecológica de los procesos que subyacen a la generación de dichos servicios (Kremen 2005). Para poder detectar la capacidad de un ecosistema de suministrar varios servicios, es necesario identificar el tipo/s de organismo/s que desempeñan un papel relevante en las propiedades de dichos ecosistemas (Kremen 2005). Precisamente en este sentido, en los últimos años se está prestando particular atención a las formas en que los diferentes organismos contribuyen al suministro de los servicios de los ecosistemas (Luck et al. 2009).

Todos los componentes de la biodiversidad (desde la diversidad genética hasta la disposición espacial de las unidades del paisaje) pueden tener un papel importante en el suministro de servicios de los ecosistemas (Díaz et al. 2006). Sin embargo, la evidencia existente apunta a que algunos de dichos componentes afectan de manera más significativa a la prestación de los servicios de los ecosistemas (Cardinale et al. 2012; Mace et al. 2012). Es este sentido, en los últimos años se ha puesto de manifiesto el rol esencial de la **diversidad funcional** sobre una gran variedad de servicios de los ecosistemas (de Bello et al. 2010). Así, parece obvio que para preservar los servicios de los ecosistemas es imperativo centrar los esfuerzos en mantener la integridad funcional de las comunidades bióticas, más allá del número de especies presentes.

1.3 Una aproximación basada en los rasgos funcionales: entendiendo los vínculos entre los impulsores de cambio y los servicios de los ecosistemas

Las investigaciones empíricas desarrolladas en las últimas décadas apuntan de manera inequívoca a que la pérdida de biodiversidad (tanto la disminución en la riqueza de especies, como la desaparición de poblaciones particulares) reduce de forma significativa la funcionalidad de los ecosistemas (Cardinale et al. 2012; Tilman et al. 2012). Además, desde la comunidad científica se asume que la biodiversidad tiene un papel esencial en el suministro de servicios de los ecosistemas (MA 2005; de Bello et al. 2010; Cardinale et al. 2012; Harrison et al. 2014), a pesar de que los vínculos concretos entre la biodiversidad y cada uno de los servicios de los ecosistemas constituyen un campo aún por explorar en mayor profundidad (Isbell et al. 2011; Balvanera et al. 2014; Bennett et al. 2015). Precisamente debido a las altas tasas de pérdida de biodiversidad registradas a nivel global (Pimm et al. 2014), y la dependencia de la población mundial de los servicios de los ecosistemas, la comprensión del papel que desempeñan las distintas dimensiones de la biodiversidad en el mantenimiento de dichos servicios se ha convertido en un objetivo prioritario (MA 2005).

Por otra parte, el conocimiento existente acerca de los vínculos entre los impulsores del Cambio Global y los procesos de los ecosistemas modulados por distintas dimensiones de la biodiversidad es aún limitado. En línea con estas limitaciones, y teniendo en

cuenta que la diversidad funcional es una de las dimensiones establecidas de la diversidad, Lavorel et al. (2007) plantearon que la comprensión de las respuestas de la biodiversidad a los impulsores de cambio, así como los efectos de la biodiversidad sobre los servicios de los ecosistemas, constituye una cuestión fundamental para poder desarrollar predicciones sobre los efectos actuales y potenciales del Cambio Global. La búsqueda de una mayor comprensión sobre estas relaciones es lo que se ha venido a denominar el **"Santo Grial" de la ecología funcional** (Lavorel y Garnier 2002). Bajo esta aproximación se busca una sola clasificación funcionalmente completa y, a la vez, suficientemente parsimoniosa que pueda abordar las complejas relaciones existentes entre los impulsores de cambio, la diversidad funcional, y sus efectos sobre las funciones y servicios de los ecosistemas (Lavorel et al. 2007).

A pesar de que existen multitud de definiciones, la mayoría coinciden en que la diversidad funcional es aquella diversidad de rasgos funcionales entre y dentro de las especies en una comunidad (Mason y de Bello 2013). En concreto, una de las definiciones más completas entiende la diversidad funcional como el valor, el rango, la distribución y la abundancia relativa de los rasgos funcionales de los organismos en una comunidad (Chapin et al. 2000; Loreau y Hector 2001; Hooper et al. 2005; Díaz et al. 2007).

La diversidad funcional establece principios, posibilitando el desarrollo de herramientas para analizar los vínculos existentes entre las comunidades biológicas y las funciones y servicios de los ecosistemas (Cornelissen et al. 2003; Lavorel et al. 2007), y permitiendo además identificar y monitorear los efectos del Cambio Global. En este sentido, parece cada vez más claro que tanto las respuestas de la biodiversidad a los impulsores de cambio como los efectos de la biodiversidad sobre los servicios de los ecosistemas pueden ser explicados mediante determinados **rasgos funcionales** (Caja 1.2).

La diversidad funcional puede medirse de múltiples formas a través de los rasgos funcionales, dependiendo de la información disponible y de los objetivos de la investigación en cuestión. Así, los rasgos funcionales pueden servir para cuantificar la diversidad funcional a través de **i) grupos funcionales**, entendidos como un subconjunto de las especies presentes en la comunidad que comparten perfiles de rasgos similares; y de **ii) índices de diversidad funcional** basados en los valores de los rasgos evaluados a nivel de especie, y que pueden incorporar ponderaciones de algunas

medidas de manera que refleje la importancia funcional de las especies en la comunidad (Fig. 1.4).

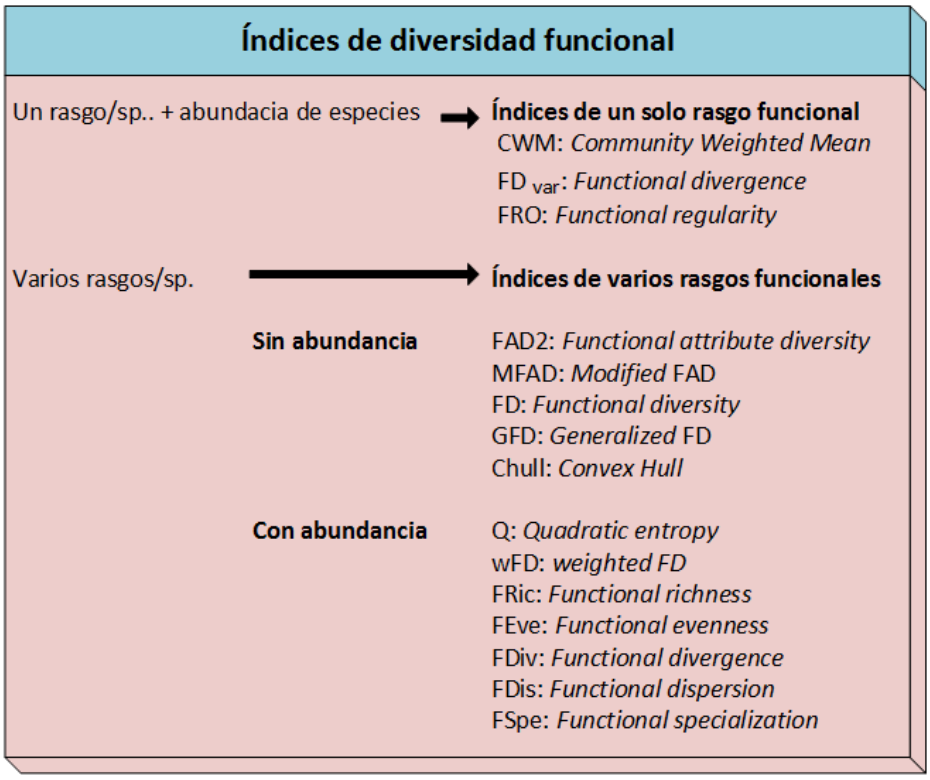

Figura 1.4 Índices de diversidad funcional más utilizados para la cuantificación de rasgos funcionales (Basado en Pla et al. 2011).

En definitiva, los rasgos funcionales determinan la respuesta del organismo a los impulsores directos de cambio ("**rasgos de respuesta**"), y sus efectos sobre los procesos o servicios de los ecosistemas ("**rasgos de efecto**") (Hooper et al. 2005; Díaz et al. 2007; de Bello et al. 2010) (Fig. 1.5; Caja 1.2). En el marco de la metáfora del "Santo Grial" de la ecología funcional, nos encontramos aquí con lo que constituiría el "*eslabón perdido*", es decir, el estudio de los solapamientos o correlaciones entre los rasgos de respuesta y de efecto. Así, la identificación de aquellos rasgos funcionales capaces de responder a los impulsores de cambio, manteniendo simultáneamente la capacidad de suministrar servicios de los ecosistemas, se dibuja como una cuestión clave para diseñar y aplicar políticas ambientales y estrategias de conservación orientadas a preservar la capacidad de recuperación de los ecosistemas (Oliver et al. 2015).

A pesar de la importancia de esta cuestión, los estudios que investigan los impactos directos de los impulsores de cambio sobre los rasgos funcionales (Devictor et al. 2010) son mucho más escasos que aquellos enfocados en los efectos sobre la diversidad taxonómica (Vilà et al. 2011; Queiroz et al. 2014). Sin embargo, existen evidencias que otorgan a los rasgos funcionales un papel determinante en los efectos sobre el funcionamiento de los ecosistemas y el suministro de diversos servicios de los ecosistemas (Díaz et al. 2006; Cadotte et al. 2011; Cardinale et al. 2012). Así, el uso de los rasgos funcionales de respuesta y de efecto se ha convertido en una herramienta con gran potencial para aplicar en las predicciones sobre el Cambio Global a varias escalas (desde los individuos a las comunidades y ecosistemas) (Suding y Goldstein, 2008).

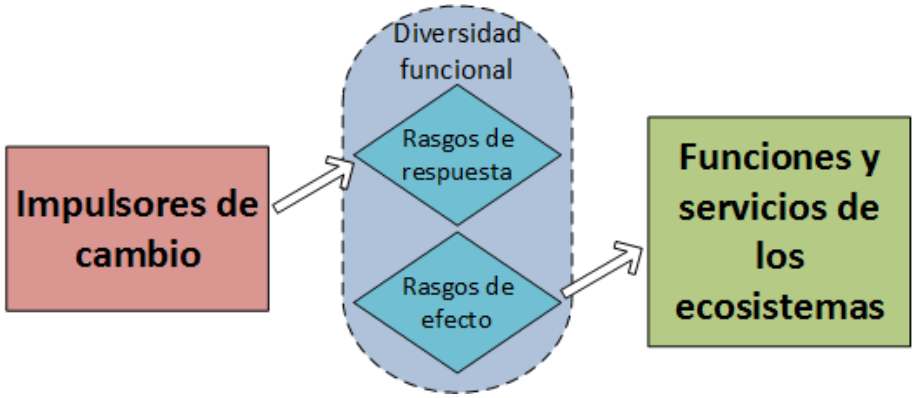

Figura 1.5 Esquema de la dirección de las relaciones entre los impulsores de Cambio Global, los rasgos funcionales (tanto los "rasgos de respuesta" como los "rasgos de efecto"), y las funciones y servicios de los ecosistemas.

El estudio de las relaciones entre los valores de riqueza de especies y la distribución y/o abundancia de los rasgos funcionales, aporta información muy útil en la comprensión de los efectos de los impulsores de cambio sobre las funciones y servicios de los ecosistemas (Naeem 2002; Mayfield et al. 2010). Precisamente a través del estudio de estas relaciones, es posible identificar la presencia de una alta o baja **redundancia funcional** (Caja 1.2). Así, cuando la redundancia funcional es alta la pérdida de algunas especies podría no repercutir significativamente en el funcionamiento del ecosistema. Al contrario, en sistemas con una baja redundancia funcional, la pérdida de unas pocas especies podría alterar significativamente la estructura y funcionamiento del ecosistema. Por tanto, los ecosistemas resilientes han de contar con una cierta redundancia funcional para poder llevar a cabo sus funciones de manera eficiente y estable a largo plazo

(Biggs et al. 2012). Esto es especialmente relevante en el contexto actual de Cambio Global, en el que se están produciendo reducciones significativas de la biodiversidad, con los consiguientes potenciales cambios en los rangos geográficos de las especies y comunidades (Barbet-Massin y Jetz 2015). En este sentido, la redundancia funcional se convierte en una variable muy interesante para explorar la **resiliencia de los ecosistemas ante el Cambio Global**.

Caja 1.2 Definiciones de los conceptos clave utilizados

- **Funciones de los ecosistemas:** procesos biológicos, geoquímicos y físicos que operan dentro de un ecosistema, manteniéndole y permitiendo el suministro de servicios de los ecosistemas. Las principales funciones de los ecosistemas incluyen el ciclo de nutrientes, la dispersión de semillas, así como muchas otras interacciones dentro y entre los componentes estructurales del ecosistema (por ejemplo: agua, suelo, biodiversidad, etc.) (Edwards et al. 2014).
- **Impulsores de cambio:** cualquier factor natural o inducido por el ser humano que causa cambios directos o indirectos sobre un ecosistema (MA 2005).
- **Impulsores directos de cambio:** impulsores de cambio que influye inequívocamente sobre los procesos de los ecosistemas (MA 2005).
- **Impulsores indirectos de cambio:** factor o conjunto de factores naturales o inducidos por los seres humanos que alteran los ecosistemas a través de su acción sobre uno o más impulsores directos de cambio (MA 2005).
- **Rasgo funcional:** característica de un organismo que tenga un vínculo con la función de dicho organismo (De Bello et al. 2010). Se trata de cualquier característica medible de un determinado organismo que está vinculada a la función de dicho organismo en el ecosistema, y que pueda ser usada comparativamente entre especies (Lavorel et al. 1997).
- **Rasgo de efecto:** aquellos rasgos que influyen en los procesos biogeoquímicos y tienen un impacto en la funcionalidad de los ecosistemas (Lavorel y Garnier, 2002; Violle et al. 2007).
- **Rasgo de respuesta:** aquellos rasgos que determinan cómo responden las especies a los cambios en las condiciones ambientales (Violle et al. 2007). Estos rasgos pueden cubrir la respuesta directa a cambios ambientales, así como cambios debidos a interacciones entre especies (Suding et al. 2008).
- **Redundancia funcional:** el número de especies que contribuyen de una manera similar a una función de los ecosistemas (Laliberté et al. 2010).
- **Servicios de los ecosistemas: c**ontribuciones directas e indirectas de los ecosistemas al bienestar humano (De Groot et al. 2010). Cualquier actividad o función de un ecosistema que suministra beneficios a los seres humanos (Mace et al. 2012).

Por otra parte, la mayoría de los vínculos conocidos entre la diversidad funcional (así como otros componentes de la biodiversidad) y los servicios de los ecosistemas se focalizan en un único nivel trófico y principalmente a escala de comunidades locales (Díaz et al. 2006). La integración de una perspectiva multi-trófica se ha contemplado desde hace unos pocos años como uno de los desafíos que es necesario afrontar para lograr un avance significativo en la investigación de las relaciones entre la biodiversidad y las funciones y servicios de los ecosistemas (Reiss et al. 2009).

En último término, las investigaciones previas así como los marcos conceptuales explicados anteriormente, nos proporcionan una base sólida que permite explorar los efectos de los impulsores de cambio sobre la diversidad funcional de organismos de diferentes niveles tróficos con el objetivo de predecir cambios en las funciones y servicios de los ecosistemas.

1.4 Objetivos de la Tesis

Son muchos los estudios realizados hasta la fecha que han explorado el impacto de los impulsores directos de cambio sobre la biodiversidad (especialmente sobre variables relacionadas con la diversidad taxonómica) (Vilà et al. 2011; Queiroz et al. 2014). Por otra parte, cada vez más investigaciones se centran en abordar también cómo afectan los impulsores directos de cambio al suministro de determinados servicios de los ecosistemas (Quétier et al. 2007; Brown et al. 2013; Orwin et al. 2015).

Sin embargo, el estudio simultáneo de las relaciones existentes entre los impulsores directos de cambio, la biodiversidad (por medio no sólo de variables de diversidad taxonómica, sino también de diversidad funcional) y los servicios de los ecosistemas, es una cuestión menos abordada por la comunidad científica. Este trabajo pretende contribuir a esclarecer la naturaleza de algunas de dichas relaciones para poder avanzar en su comprensión (Fig. 1.6).

Figura 1.6 Nube de palabras elaborada a partir de los conceptos clave más utilizados a lo largo del presente capítulo. El tamaño de las palabras es directamente proporcional al número de veces que haya sido utilizada en el texto.

El **objetivo general** de la presente Tesis Doctoral es *contribuir a la comprensión de los efectos de los impulsores directos de cambio sobre la diversidad (taxonómica y funcional) de distintos grupos de organismos, y su traducción en el suministro de servicios de los ecosistemas*. Se persigue no sólo recopilar las evidencias empíricas ya identificadas acerca de algunas de estas interacciones, sino también aportar nuevos casos de estudio que contribuyan a ampliar la comprensión del funcionamiento, dirección, e intensidad de los vínculos entre impulsores directos de cambio, biodiversidad y servicios de los ecosistemas.

Para la consecución de ese objetivo principal, se plantean los siguientes **objetivos específicos**:

1. Analizar el estado del conocimiento existente a nivel global acerca de los vínculos entre los impulsores directos de cambio y los servicios de los ecosistemas, mediados por rasgos funcionales de distintos grupos de organismos.

2. Analizar el efecto del abandono y la intensificación del uso del suelo en los agroecosistemas mediterráneos sobre la diversidad (taxonómica y funcional) de varios grupos de organismos.
3. Explorar de manera empírica, a través de un caso de estudio, las relaciones existentes entre el uso del suelo y el servicio de polinización en un contexto de agroecosistemas mediterráneos.

1.5 Estructura de la Tesis

La presente Tesis Doctoral se estructura en cuatro capítulos de resultados con identidad propia. Cada uno de ellos pretende responder a alguno de los distintos objetivos planteados en esta investigación, tal y como muestra la Figura 1.7.

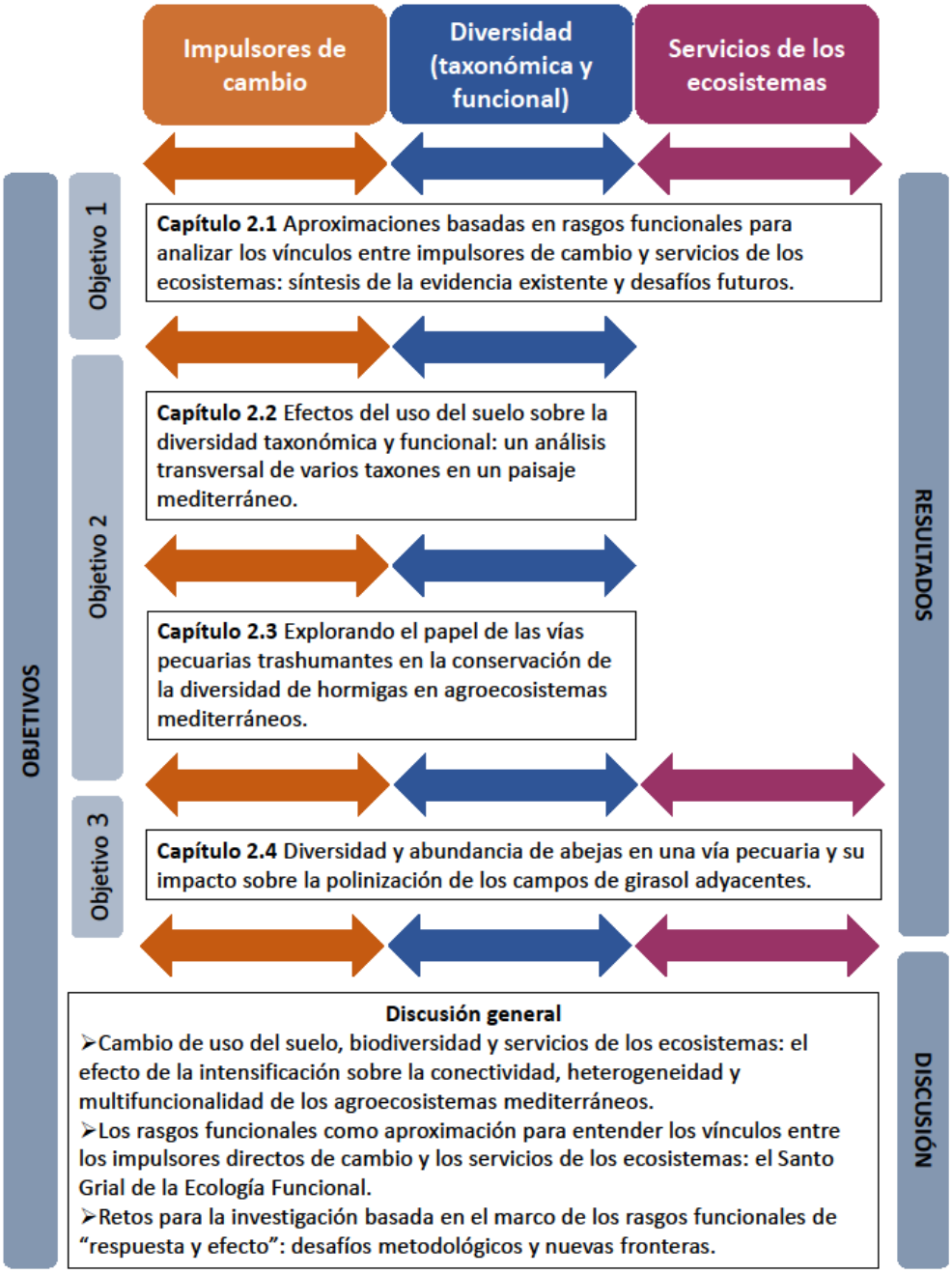

Figura 2.7 Estructura de la Tesis Doctoral donde se vinculan los objetivos planteados en la investigación con los cuatro capítulos de resultados.

El **Capítulo 2.1** (*Aproximaciones basadas en rasgos funcionales para analizar los vínculos entre impulsores de cambio y servicios de los ecosistemas: síntesis de la evidencia existente y desafíos futuros*) aborda el objetivo 1, y constituye un análisis exploratorio, a través de una revisión bibliográfica sistemática, acerca del "estado del arte" en el estudio de los vínculos existentes entre los impulsores directos de cambio,

los rasgos funcionales de tres grupos de organismos (plantas, invertebrados y vertebrados) y los servicios de los ecosistemas. Mediante el análisis de 125 artículos científicos: (1) se muestran las tendencias en dicha investigación, y (2) se sintetiza la evidencia empírica existente hasta la fecha en que concluye dicho trabajo (el año 2014, inclusive). De esta forma, se trata de identificar vacíos de conocimiento en la literatura científica y desafíos de futuro.

El **Capítulo 2.2** (*Efectos del uso del suelo sobre la diversidad taxonómica y funcional: un análisis transversal de varios taxones en un paisaje mediterráneo*) aborda el segundo objetivo, y consiste en el estudio y comparación de la diversidad taxonómica y funcional de cuatro grupos bióticos (hormigas, aves, vegetación herbácea y vegetación leñosa) a dos escalas espaciales a lo largo de cuatro tipos de uso del suelo en un gradiente de intensificación (monte mediterráneo, dehesas, bosque de pinar mixto, y olivares) en Sierra Morena (Jaén).

El **Capítulo 2.3** (*Explorando el papel de las vías pecuarias trashumantes en la conservación de la diversidad de hormigas en agroecosistemas mediterráneos*) contribuye también a la consecución del segundo objetivo. En este capítulo se realiza una comparación de la diversidad (taxonómica y funcional) de hormigas presente en un tramo de la Cañada Real Conquense (con uso ganadero trashumante), frente a un tramo cercano de la Cañada Real Murciana (donde el uso ganadero se abandonó hace más de tres décadas). Además, se explora el efecto de dichas vías pecuarias sobre la diversidad de hormigas en los campos de cultivo adyacentes (viñedos y cultivos herbáceos) en un paisaje mediterráneo con predominancia de agricultura intensiva.

El **Capítulo 2.4** (*Diversidad y abundancia de abejas en una vía pecuaria y su impacto sobre la polinización de los campos de girasol adyacentes*) aborda, en forma de caso de estudio, el tercer objetivo. Consiste en el análisis de la comunidad de abejas en la Cañada Real Conquense, y la evaluación del efecto de dicha comunidad de abejas sobre el servicio de polinización y la producción agrícola en los campos intensivos de girasol adyacentes a esta vía pecuaria.

1.6 Aproximación metodológica

Los métodos utilizados se presentarán detalladamente en cada una de las secciones del capítulo de resultados. Sin embargo, de cara a proporcionar una visión general de las

diferentes aproximaciones metodológicas utilizadas en la Tesis, se presenta a continuación una tabla que resume los principales métodos y análisis aplicados a lo largo del trabajo (Tabla 1.1).

Para la obtención de los datos necesarios, se llevó a cabo una revisión bibliográfica sistemática y diversas campañas de campo. La **revisión bibliográfica sistemática** implicó una dedicación completa durante dos meses para realizar una exploración exhaustiva de las cuestiones planteadas en la primera sección de resultados, así como diseñar y ejecutar posteriores filtros que facilitaran una base de datos ajustada a los objetivos planteados.

El **trabajo de campo** de esta Tesis se realizó entre los años 2011 y 2013, en dos áreas de estudio: la Cañada Real Conquense y Sierra Morena Oriental (Fig. 1.8). Estas zonas se describirán en mayor detalle en cada capítulo correspondiente de resultados.

El trabajo de campo consistió en:

- *Siete salidas de campo exploratorias* de 2-4 días de duración, entre uno y dos meses antes de los muestreos definitivos correspondientes a cada uno de los tres casos de estudio empíricos. El objetivo de estas salidas fue explorar en profundidad de las zonas de estudio (Fig. 1.7) para adecuar el diseño muestral a las características de cada zona en base a las preguntas de investigación.
- *Nueve campañas de muestreo* de entre 2 días y 2 semanas de duración, utilizando distintos métodos de muestreo de los grupos taxonómicos estudiados, que serán descritos con mayor detalle en cada sección correspondiente.

Los análisis de datos incluyen un abanico amplio de metodologías, que van desde los test de comparaciones simples (ANOVA, NMDS, o diversos test no paramétricos) hasta análisis multivariantes (p.e. RDA) y modelos lineales mixtos (ver Tabla 1.1).

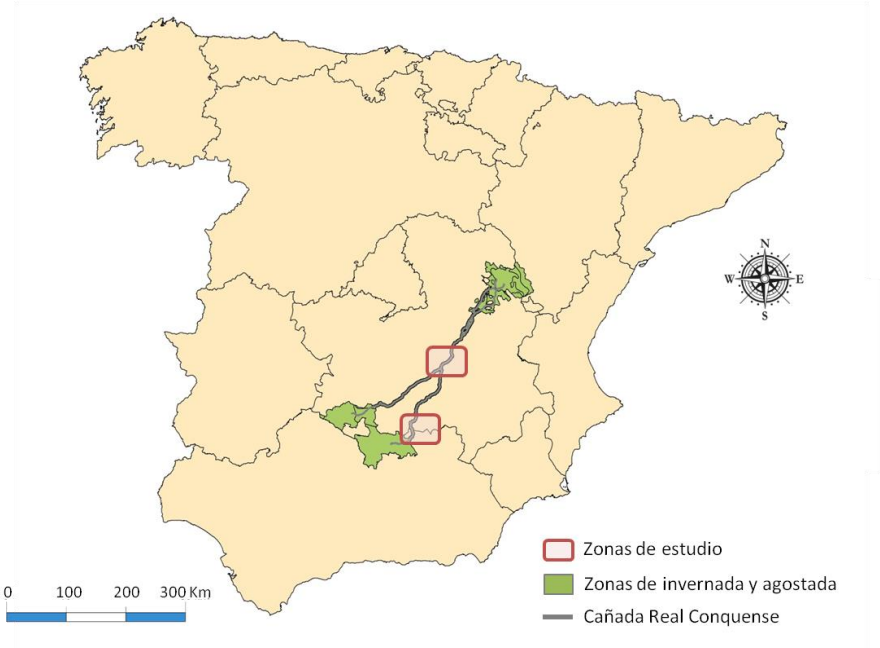

Figura 1.8 Mapa del territorio nacional donde se localizan las zonas de estudio, que se describirán con mayor detalle en cada capítulo de resultados.

Tabla 1.1. Síntesis de los principales métodos y análisis de datos utilizados en el desarrollo de la investigación.

Capítulo	Área(s) de estudio	Toma de datos	Análisis de datos
2.1		○ Revisión bibliográfica sistemática (ISI Web of Science).	○ Análisis descriptivos. ○ Análisis de redundancia (RDA). ○ Test de permutaciones (Monte Carlo).
2.2	Sierra Morena oriental (Jaén): municipios de Aldeaquemada, Santa Elena, Vilches, Navas de San Juan and Santisteban del Puerto.	○ Identificación *in situ* de especies herbáceas y leñosas. ○ Estaciones de escucha para identificación de aves. ○ Instalación de trampas *pitfall* para hormigas. ○ Identificación de especies de hormigas y medición de sus rasgos funcionales en laboratorio. ○ Búsqueda de rasgos funcionales de vegetación a través de bases de datos.	○ Cálculo de índices de diversidad (Índice de Simpson) y diversidad funcional (Índice de Rao). ○ Cálculo de un modelo lineal mixto. ○ Tests *post hoc* (Tukey).
2.3	Cañada Real Conquense y Cañada Real Murciana: municipios de Las Pedroñeras, Casa de los Pinos y Villarobledo (Castilla La-Mancha).	○ Instalación de trampas *pitfall* para el muestreo de hormigas. ○ Identificación de especies de hormigas y medición de rasgos funcionales en laboratorio. ○ Búsqueda bibliográfica para la obtención de valores para los rasgos funcionales de hormigas.	○ Análisis de la composición de especies a través de un escalado multidimensional (NMDS). ○ Cálculo de riqueza de especies. ○ Cálculo de índice de diversidad funcional (Índice de Rao). ○ Tests MANOVA, ANOVA.
2.4	Cañada Real Conquense: municipios de Altarejos, San Lorenzo de la Parrilla, Belmontejo, Cervera del Llano, Villalgordo del Marquesado, y Villar de la Encina (Castilla La-Mancha).	○ Instalación de *pantraps* para el muestreo de abejas. ○ Muestreo visual *in situ* de abejas. ○ Identificación de especies de abejas y medición de rasgos funcionales en laboratorio. ○ Recolección de capítulos de girasol. ○ Identificación *in situ* de especies herbáceas y leñosas.	○ Análisis de la composición de especies a través de un escalado multidimensional (NMDS). ○ Cálculo de riqueza, abundancia, y tasa de visitas al girasol de abejas ○ Cálculo del porcentaje de vaneamiento como indicador de producción de semillas de girasol. ○ Modelo mixto lineal generalizado (GLMM).

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Capítulo 2

Resultados

2.1 Aproximaciones basadas en rasgos funcionales para analizar los vínculos entre impulsores de cambio y servicios de los ecosistemas: sintetizando la evidencia existente y retos futuros

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Capítulo 2.1

Aproximaciones basadas en rasgos funcionales para analizar los vínculos entre impulsores de cambio y servicios de los ecosistemas: sintetizando la evidencia existente y retos futuros

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2.1 Trait-based approaches to analyse links between the drivers of change and ecosystem services: synthesising existing evidence and future challenges

Summary

1. Understanding the responses of biodiversity to drivers of change and the effects of biodiversity on ecosystem properties and ecosystem services is a key challenge in the context of global environmental change.
2. We performed a systematic review and meta-analysis of the scientific literature linking direct drivers of change and ecosystem services via functional traits of three taxonomic groups (vegetation, invertebrates and vertebrates) to: (a) uncover trends and research biases in this field and (b) synthesise existing empirical evidence.
3. Our results show the existence of important biases in published studies related to ecosystem types, taxonomic groups, direct drivers of change, ecosystem services, geographical range and the spatial scale of analysis. We found multiple evidence of links between drivers and services mediated by functional traits, particularly between land-use changes and regulating services in vegetation and invertebrates.
4. Seventy-five functional traits were recorded in our sample. However, few of these functional traits were repeatedly found to be associated with both the species responses to direct drivers of change (response traits) and the species effects on the provision of ecosystem services (effect traits).
5. Our results highlight the existence of potential "key functional traits", understood as those that have the capacity to influence the provision of multiple ecosystem services, while responding to specific drivers of change, across a variety of systems and organisms. Identifying "key functional traits" would help to develop robust indicator systems to monitor changes in biodiversity and their effects on ecosystem functioning and ecosystem services supply.

Keywords: Biodiversity, Ecosystem Function, Effect Trait, Global Environmental Change, Response Trait, Systematic Review

2.1.1 Introduction

Global biodiversity is being severely affected by drivers of change that are directly or indirectly induced by human activities. Direct drivers of change include land use change, climate change, invasive alien species, overexploitation and pollution (Vitousek et al. 1997; Pereira et al. 2012). The loss of biodiversity may alter ecosystem functioning and the delivery of ecosystem services, with major repercussions on human well-being (Balvanera et al. 2006; Hanski et al. 2012; Mace et al. 2012; Dirzo et al. 2014). Although biodiversity is assumed to be critical for providing ecosystem services (de Bello et al. 2010; Cardinale et al. 2012; Harrington et al. 2014), our understanding about the links between biodiversity and individual ecosystem services remains incomplete (Suding et al. 2008; Isbell et al. 2011; Balvanera et al. 2014; Bennett et al. 2015). Lavorel et al. (2007) suggested that understanding the responses of biodiversity to drivers and the effects of biodiversity on ecosystem services is critical for developing future scenarios about the effects of global environmental change. Yet, our knowledge about the linkages between specific drivers of change and ecosystem properties modulated by biodiversity remains limited.

It has become increasingly clear that both the responses of biodiversity to drivers of change and the effects of biodiversity on ecosystem services may be explained by functional traits (Díaz et al. 2007). Functional traits determine the organism's response to pressures and drivers of change (response traits) and its effects on ecosystem properties and the provision of ecosystem services (effect traits) (Hooper et al. 2005; de Bello et al. 2010; Cadotte et al. 2011; Valiente-Banuet et al. 2015). Recent trait-based approaches have assessed how ecosystem services might be affected by drivers of change (Quétier et al. 2007) through the analysis of effect and response traits (Lavorel & Garnier 2002; Díaz et al. 2007, 2013; Suding et al. 2008; Lavorel et al. 2011; Lavorel 2013). These trait-based approaches might prove effective for improving ecosystem management and decision-making within the context of environmental change (Lavorel 2013; Nagendra et al. 2013).

Here, we performed a systematic literature review and meta-analysis to synthesise existing empirical evidence about the interlinkages among direct drivers of change and ecosystem services, mediated by functional traits of three taxonomic groups (vegetation, invertebrates and vertebrates). There have been several scientific literature reviews on

how the direct drivers of change are linked with functional traits (e.g., Verheyen et al. 2003) or how functional traits are linked with ecosystem services (e.g., de Bello et al. 2010; Harrison et al. 2014; Ricketts et al. 2016). However, to the best of our knowledge, this work presents the first systematic review on the entire pathway, from drivers to ecosystem services via traits, across different taxonomic groups.

First, we reviewed the status and general trends in the scientific literature to characterise the "research landscape" in this field until 2014. Second, we compiled and synthesised existing evidence of relationships among drivers of change, functional traits and ecosystem services. Then, we explored the existence of "bundles of traits" associated to particular direct drivers of change and ecosystem services. Finally, we identified existing knowledge gaps, and suggested future challenges in the application of trait-based approaches for biodiversity monitoring.

2.1.2 Materials and methods

Literature search

We conducted a Web of Science survey up to 2014, using search terms related to functional traits (N = 29 terms), combined with direct drivers of change (N = 33 terms) and ecosystem services and all potential synonyms (N = 72 terms) (see Appendix S1, Supporting information for the complete list of the keywords used in the systematic review). We acknowledge that our search terms might include some publications that focus on ecosystem functions, ecological processes or benefits, which, under certain definitions, would not properly qualify as "ecosystem services". Basically, the ecosystem services concept is complex and subject to multiple interpretations (Nahlik et al. 2012; Abson et al. 2014). Given that there is not yet a single, unifying definition of ecosystem services (Nahlik et al. 2012), here, we embraced the proposal of Mace et al. (2012): "an activity or function of an ecosystem that provides benefit to humans". This definition encompasses the entire pathway from ecological processes to final ecosystem services, being the one that best fits with the approach of our review. Thus, we selected sufficiently broad enough search terms to include all ecosystem functions/services identified in the Millennium Ecosystem Assessment (MA) and the Common International Classification of Ecosystem Services (CICES; http://cices.eu/).

The literature search resulted in a sample of 302 papers, of which 125 fit the criteria for inclusion, that is, papers that have empirically used trait-based approaches to analyse links between the drivers of change and ecosystem services. Appendix S2 (Supporting information) shows the diagram flow of the methodological process.

Data collection

Following the content analysis of these selected papers, two databases were created. The first database (N = 125 papers; see Appendix S3, Supporting information, for the complete list of publications) was used to characterise the current state and trends of trait-based ecosystem services research, including information on: (a) publication characteristics (i.e. year of publication, type of research), (b) study area, (c) methodological approach used (e.g. data source, theoretical or analytical approach), (d) taxonomic group studied, (e) ecosystem type, (f) direct drivers of change analysed, (g) functional traits used, (h) category of ecosystem services (i.e. provisioning, regulating or cultural) and (i) specific ecosystem services investigated. Appendix S4 (Supporting information) summarises the list of attributes used to characterise publications.

The second database was traits-oriented and only considered those statistically significant relationships among drivers of change, functional traits and ecosystem services found in the existing literature (N = 83 observations, from 71 papers). In this database, we codified (as dummy variables) those relationships between drivers and response traits, and/or between effect traits and ecosystem services, for those studies that reported significant evidence. As we could not incorporate any weighting of the magnitude of the responses and/or effects, we acknowledge that this might result in an overrepresentation of those functional traits that have been most frequently investigated.

Data analysis

To address the current status and trends of research in this field, we performed frequency analyses on ecosystem types, taxonomic groups, functional traits, direct drivers of change, and ecosystem services (using the first database). After analysing research trends, we focused on synthesising the existing evidence of links between drivers and ecosystem services mediated by functional traits (using the second

database). In doing so, we first analysed emerging patterns, focusing particularly on how land use change affects regulating services, which is the relationship that has been most extensively tested using functional traits.

To draw general conclusions from existing evidence of interlinkages between drivers of change and functional traits, as well as between functional traits and ecosystem services, we conducted six different redundancy analyses (RDA). Three RDAs were performed to synthesise the evidence of interlinkages between direct drivers of change (used as explanatory variables) and response traits (as dependent variables) for each of the three taxonomic groups. Then, three other RDAs were performed to synthesise the existing evidence linking effect traits (used as explanatory variables) and ecosystem services (as dependent variables). In all analyses, the dependent and explanatory variables were dichotomous according to the existence of evidence about relationships between drivers of change and response traits and between effect traits and ecosystem services. A Monte Carlo permutation test (500 permutations) was performed to determine the significance of explanatory variables. RDA analyses were performed using XLSTAT 2012 (Addinsoft) software.

3.1.3 Results

Status and trends in trait-based ecosystem services research

Temporal trends in our sample show that this topic is an emerging research field, with an exponential increase in the number of trait-based papers that contrast with the arithmetic increase in ecology research (Fig. 2.1.1). Although the first empirical trait-based study was published in 2001 (i.e. Dukes 2001), the number of papers grew exponentially between 2008 (N =5) until 2012 (N =27), but plateaued during 2013 and 2014.

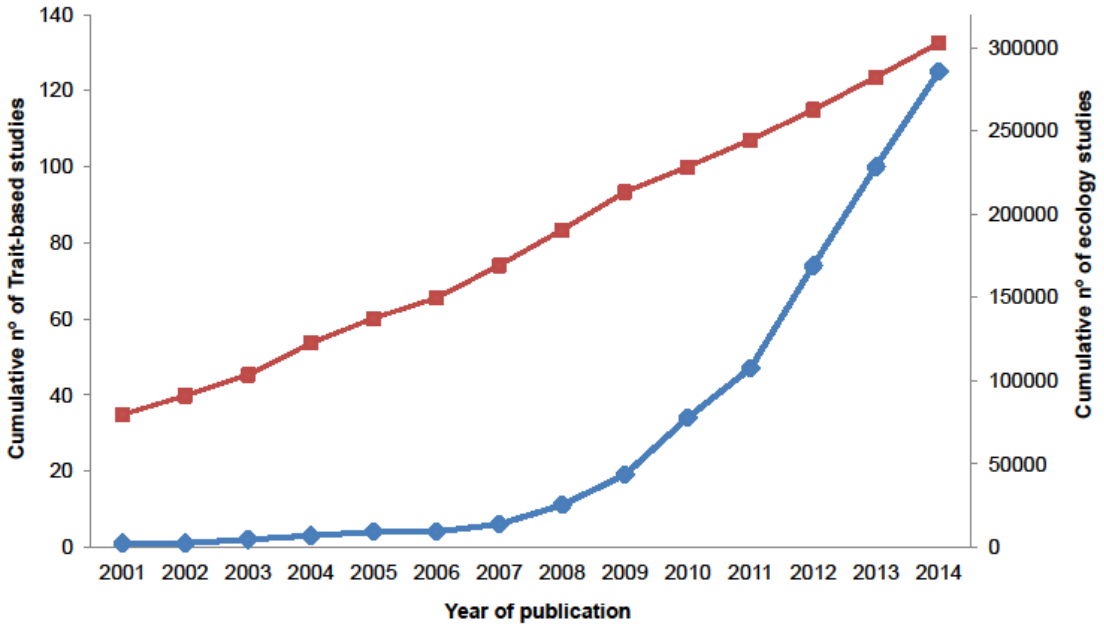

Figure 2.1.1. Trends in the scientific literature exploring the links among drivers of change, functional traits and ecosystem services, compared with general trends in ecology scientific literature. Blue line indicates the cumulative number of studies considered in this systematic review along our study period (Y axis on the left side). Red line indicates the cumulative number of ecology studies along our study period (Y axis on the right side). The general trend of ecology research was obtained by a survey up to 2014 in the Web of Science, using "ecology" or "ecolog*" as search terms.

Most publications corresponded to cultivated agroecosystems (35.9%), forests (21.1%) and dryland ecosystems (11.0%) (Fig. 2.1.2a). Most studies were conducted at a local (60.3%) or national (34.0%) scale, with very few being conducted at regional or global scales (Fig. 2.1.2b). Most of the research was conducted in Europe (38.9%), followed by North America and Oceania (14.1% and 8.8%, respectively) (Fig. 2.1.2c). Most studies in our sample (57.7%) were based on primary data, while the remainder used secondary sources (14.6%) or a mix of both data types (27.6%) (Fig. 2.1.2d). Vegetation and invertebrates (i.e. insects) were the most studied taxonomic groups (40.4% and 37.4% of the sampled papers, respectively), with research on vertebrates being scarcer (16.6%) (Fig. 2.1.2e).

Land use change was the most frequently studied driver of change in our sample, with 67.8% of the studies only focusing on analysing this specific driver and its effects. Studies on invasive alien species and climate change were also relevant in our sample (11.8% and 10.1%, respectively). In contrast, the interlinkages between other drivers,

such as pollution or overexploitation, and ecosystem services via functional traits have been rarely examined. Only five studies were recorded that simultaneously analysed the effect of various drivers of change (Fig. 2.1.2f).

Most studies focused on exploring regulating services (62.1%), followed by provisioning services (19.2%), whereas studies on cultural services were scarce (9.3%). Again, few studies simultaneously assessed more than one category of ecosystem services (Fig. 2.1.2g). Finally, most papers investigated only one (65.8%) or two ecosystem services (23.0%), with just 11.1% of studies assessing more than two ecosystem services (Fig. 2.1.2h).

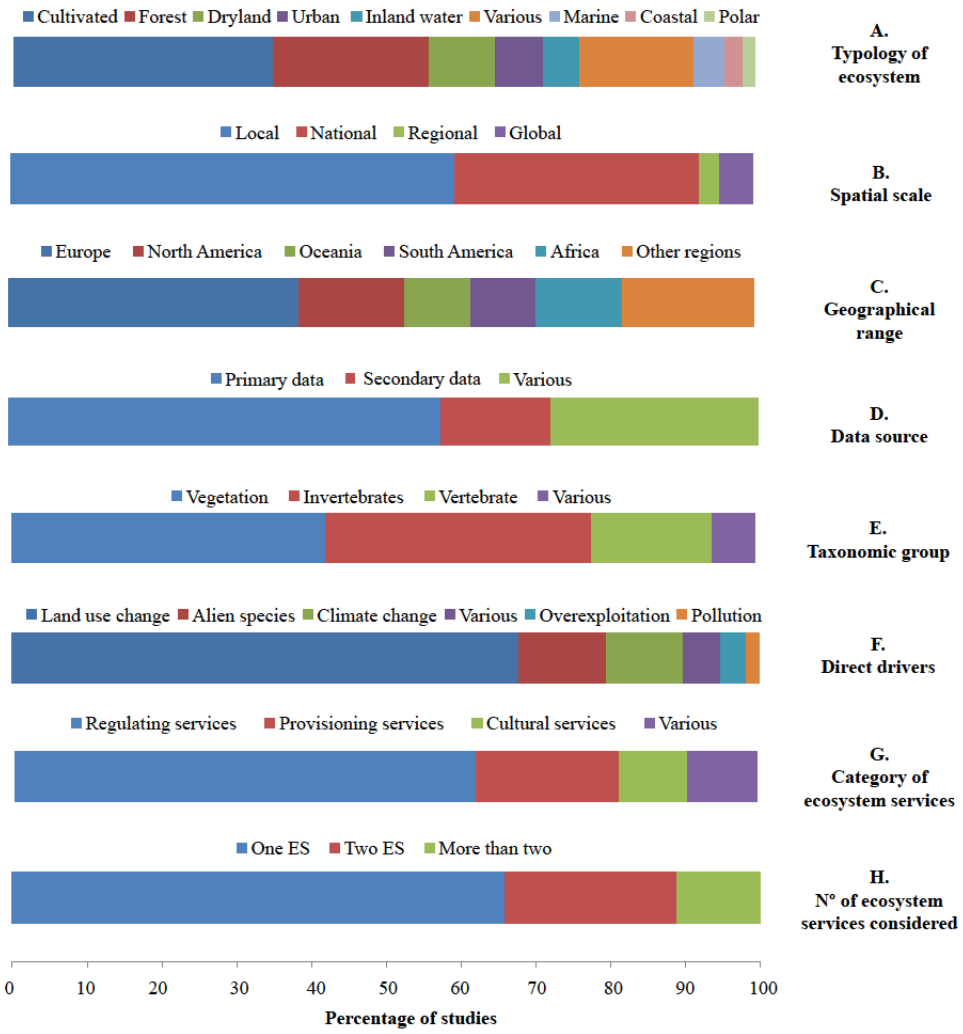

Figure 2.1.2. Characterisation of the peer-reviewed literature sample (N = 125) according to the percentage of studies: (a) conducted on each type of ecosystem; (b) conducted at different spatial scales; (c) conducted at different geographical regions; (d) using different data sources; (e) focusing on each taxonomic group; (f) analysing each direct driver of change; (g) analysing

each category of ecosystem services; and (h) according to the number of ecosystem services considered.

A total of 75 functional traits were recorded in our dataset: 41 for vegetation, 25 for invertebrates and 20 for vertebrates (Appendix S5, Supporting information). The most frequently investigated trait was size, which was used for all three analysed taxonomic groups. The next most frequently investigated trait was diet for vertebrates and invertebrates, followed by habitat dependency (mostly for vertebrates and invertebrates), dispersal activity (for all three groups) and growth form (for vegetation) (Fig. 2.1.3).

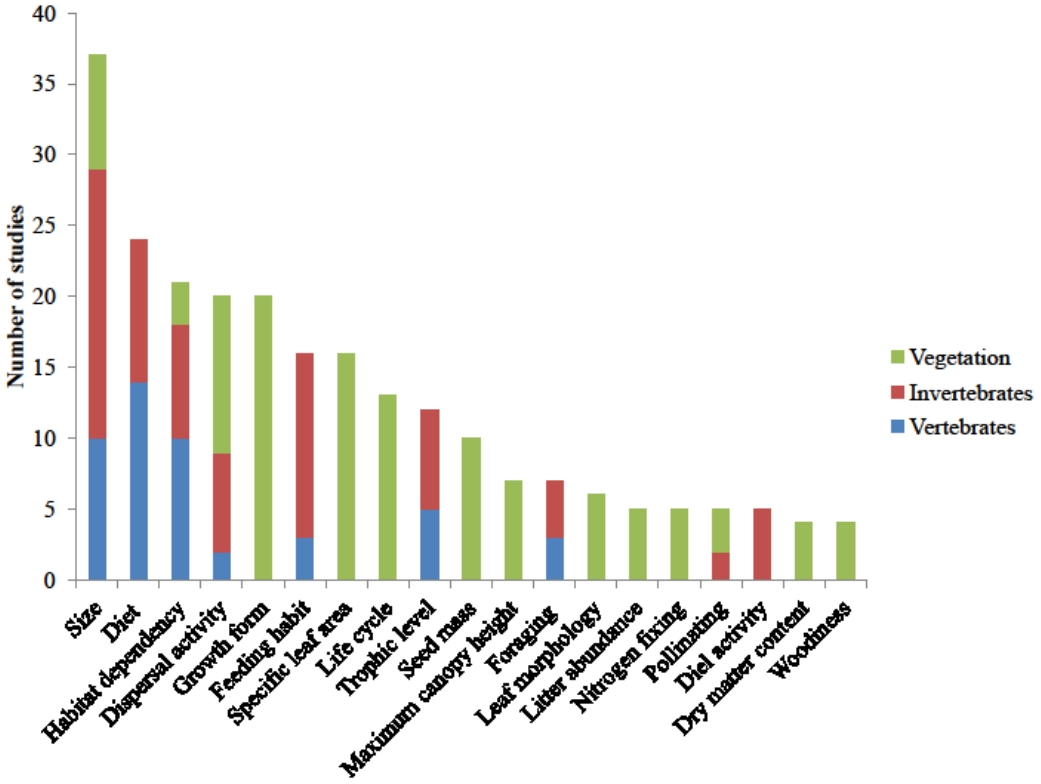

Figure 2.1.3. Number of studies using each of the most frequently analysed functional traits (only those traits used in more than three papers are represented) in the scientific literature for the three taxonomic groups.

Research linking direct drivers of change, functional traits and ecosystem services

The relationships between land use change and regulating services were clearly the most frequently addressed using a trait-based approach (73.6% of the papers; Fig. 2.1.4),

particularly for links mediated by vegetation and invertebrate traits. Amongst regulating services potentially affected by land use change via functional traits, habitat provision, pest control and nutrient cycling were the most analysed. Relationships of land use change with provisioning services have also been largely explored in the published literature (28.0% of the papers), particularly with respect to food provision via vegetation and invertebrate traits.

After land use change, climate change and invasive alien species were the drivers that received the most attention in the scientific literature. Studies on the links between alien species and regulating and provisioning services mainly focused on invasion resistance mediated by vegetation traits. The scientific literature mostly explored the impacts of climate change on provisioning and regulating services, particularly those mediated by vertebrate traits (Fig. 2.1.4).

Our results show that few studies have focused on how overexploitation affects provisioning services mediated by vertebrate traits (particularly of fish) or regulating services, such as invasion resistance, mediated by plant traits. Studies exploring the relationship between pollution and ecosystem services are also limited, and mostly focused on the effects of water pollution on food production mediated by vertebrate traits (Fig. 2.1.4).

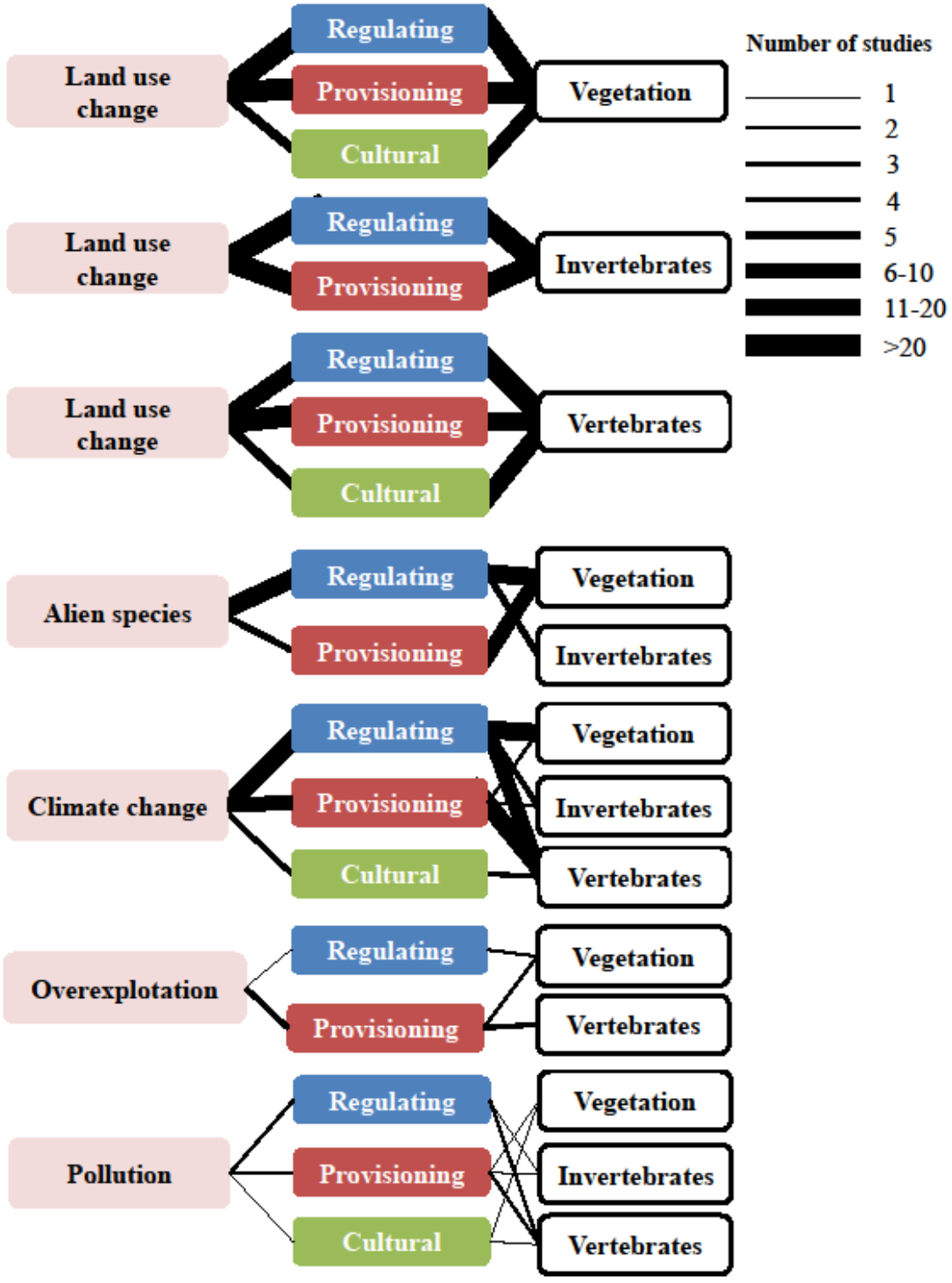

Figure 2.1.4. Number of studies in the sample that empirically explored the impacts of the drivers of change on ecosystem services mediated by the functional traits of each of the three taxonomic groups. In the case of land use change, the links are presented separately for each taxonomic group, to facilitate figure readability.

Synthesising evidence of links among drivers of change, functional traits and ecosystem services

Twelve vegetation traits were found to respond to land use change and influence six regulating services and four provisioning services. Two vegetation traits were also found to respond to climate change, while another two vegetation traits responded to alien species (Fig. 2.1.5A). For invertebrates, nine traits were found to respond to land use change, while three traits responded to climate change. These traits were found to affect seven regulating services and one provisioning service (Fig. 2.1.5B). For vertebrates, six traits were found to respond to land use change, while two traits responded to overexploitation. These traits affected five regulating services and one provisioning service (Fig. 2.1.5C).

Overall, 84.2% of the traits analysed acted both as response and effect traits; specifically, 90.4% for vegetation, 75.0% for invertebrates and 87.5% for vertebrates (Fig. 2.1.5).

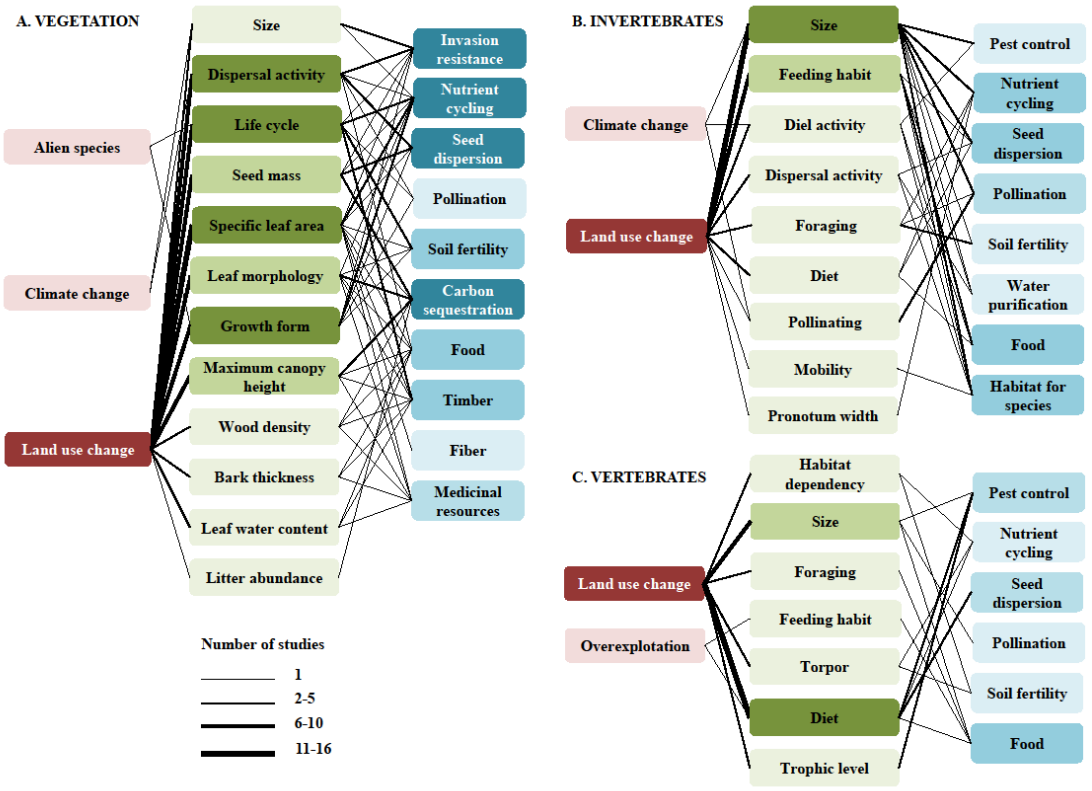

Figure 2.1.5. Functional traits for which empirical evidence has been found of links with drivers of change (acting as response traits) and with ecosystem services (acting as effect traits) for all three taxonomic groups. Line width indicates the number of studies reporting significant

results for that relationship. Red boxes refer to the drivers of change, green boxes to the functional traits, and blue boxes to the ecosystem services. Box colour intensity increases according to the number of studies reporting significant links with that variable.

The most frequent vegetation traits that showed significant links with land use change and ecosystem services were size, dispersal activity, specific leaf area, life cycle, seed mass, nitrogen fixing, leaf morphology, growth form, maximum canopy height and woodiness. All of these traits acted as both response traits to land use change and effect traits on certain regulating services, such as nutrient cycling and soil fertility (see Table 2.1.1). In the case of invertebrates, size and feeding habit were the most common traits showing significant relationships with land use change. These traits also influenced several regulating services (Table 2.1.1), such as water purification and seed dispersion, acting as both response and effect traits. For vertebrates, not enough studies were available to derive any clear conclusion, although size, diet, foraging and habitat dependency appeared to be affected by land use change. These traits influenced certain regulating services, such as pest control and pollination (in the case of size) and seed dispersion (in the case of diet).

Table 2.1.1. Number of studies that found a relationship between land use change and ecosystem services via functional traits (specifying, for each trait, the number of cases (N) where it acts as response or effect trait). Only those traits with 2 or more cases have been presented. For the complete list of traits and the number of studies, see Appendix E. (SLA: specific leaf area).

Taxa	Traits	Response trait (N)	Effect traits (N)	Ecosystem Service	Study type
Vegetation	Size	2	1	Nutrient cycling	Obs
			1	Invasion resistance	Obs
	Dispersal activity	6	1	Invasion resistance	Obs
			1	Seed dispersion	Obs
			1	Nutrient cycling	Obs
			1	Pollination	Obs
	SLA	9	3	Nutrient cycling	Obs
			1	Soil fertility	Pred
			1	Seed dispersion	Obs
			3	Raw materials	Obs
			1	Carbon cycling	Obs

		1	Medicinal resources	Obs
Life cycle	7	3	Nutrient cycling	Obs
		2	Soil fertility	Pred
		1	Pollination	Obs
Seed mass	6	1	Invasion resistance	Obs
		2	Nutrient cycling	Obs
		2	Seed dispersion	Obs
		1	Carbon cycling	Obs
Nitrogen fixing	2	1	Nutrient cycling	Obs
		1	Raw materials	Obs
Leaf morphology	3	1	Carbon cycling	Obs
		2	Raw materials	Obs
		1	Nutrient cycling	Obs
		1	Soil fertility	Obs
		1	Medicinal resources	Obs
Growth form	2	2	Nutrient cycling	Obs

			1	Soil fertility	Obs
	Maximum canopy height	3	2	Carbon cycling	Obs
			2	Raw material	Obs
			1	Medicinal resources	Obs
	Woodiness	3	1	Carbon cycling	Obs
			2	Raw materials	Obs
			1	Medicinal resources	Obs
Invertebrates	Size	9	2	Soil fertility	Obs
			2	Seed dispersion	Obs
			3	Pest control	Obs
			2	Nutrient cycling	Obs
			1	Water purification	Obs
			2	Pollination	Obs
			1	Waste treatment	Obs
	Feeding habit	4	1	Water purification	Obs
			1	Seed dispersion	Obs

			1	Food	Obs
			1	Habitat for species	Obs
	Diet	2	2	Nutrient cycling	Obs
			2	Seed dispersion	Obs
	Foraging	3	1	Nutrient cycling	Obs
			1	Soil fertility	Obs
			1	Pollination	Obs
	Dispersal activity	3	1	Habitat for species	Obs
			1	Water purification	Obs
			1	Seed dispersion	Obs
Vertebrates	Size	2	1	Pest control	Obs
			1	Nutrient cycling	Obs
			1	Soil fertility	Obs
			1	Pollination	Obs
			1	Cultural services*	Obs
	Diet	5	3	Seed dispersion	Obs

		1	Pest control	Obs
		1	Nutrient cycling	Obs
		1	Soil fertility	Obs
Foraging	2	1	Nutrient cycling	Obs
		1	Soil fertility	Obs
Habitat dependency	3	1	Seed dispersion	Obs
		1	Nutrient cycling	Obs
		1	Soil fertility	Obs

Uncovering bundles of traits associated to particular direct drivers of change and ecosystem services

RDAs analyses of the relationship between direct drivers of change and response traits revealed different bundles for each taxonomic group (Fig. 2.1.6A, C, E; Appendix S6, Supporting information). For vegetation, land use change was related to specific leaf area in the negative F1 scores, while alien species and overexploitation were related to life cycle and parasitism in the positive scores. In F2, climate change was related with size and dispersal activity in the positive scores (Fig. 2.1.6A).

For invertebrates, climate change appeared to be strongly related with diel activity and pollinating in the positive F1 scores (Fig. 2.1.6C). For vertebrates, land use change was related to size (negative F1 scores), while overexploitation was related to feeding habit (positive F1 scores) (Fig. 2.1.6E).

RDAs analyses of the relationship between effect traits and ecosystem services also showed different bundles for each taxonomic group (Fig. 2.1.6B, D, F; Appendix S7, Supporting information). For vegetation, positive F1 scores showed relationships between size, leaf morphology, life cycle, storage organs, root morphology and growth form with soil fertility and nutrient cycling (Fig. 2.1.6B). Many vegetation effect traits (litter abundance, maximum canopy height, woodiness, vegetative reproduction, growth rate, nitrogen content and diameter at breast height) had negative F1 scores and positive F2 scores related with carbon cycling. Negative F2 scores for pollinating were related with pollination service and invasion resistance (Fig. 2.1.6B).

For invertebrates, positive F1 scores showed a bundle of different effect traits (pronotum width, diet, size, habitat dependency, foraging, and microclimate moisture preference) with nutrient cycling and soil fertility. Negative F2 scores were obtained for diel activity and mobility linked with habitat for species, whereas positive F2 scores were obtained for size and diet related to seed dispersion and water purification (Fig. 2.1.6D).

The specific RDA for vertebrates revealed a relationship between diet, habitat dependency and torpor with nutrient cycling and soil fertility in the positive F1 scores. In the negative F1 scores, size and trophic level relate to pest control and seed dispersion. Diet was related with seed dispersion in the positive F2 scores (Fig. 2.1.6F).

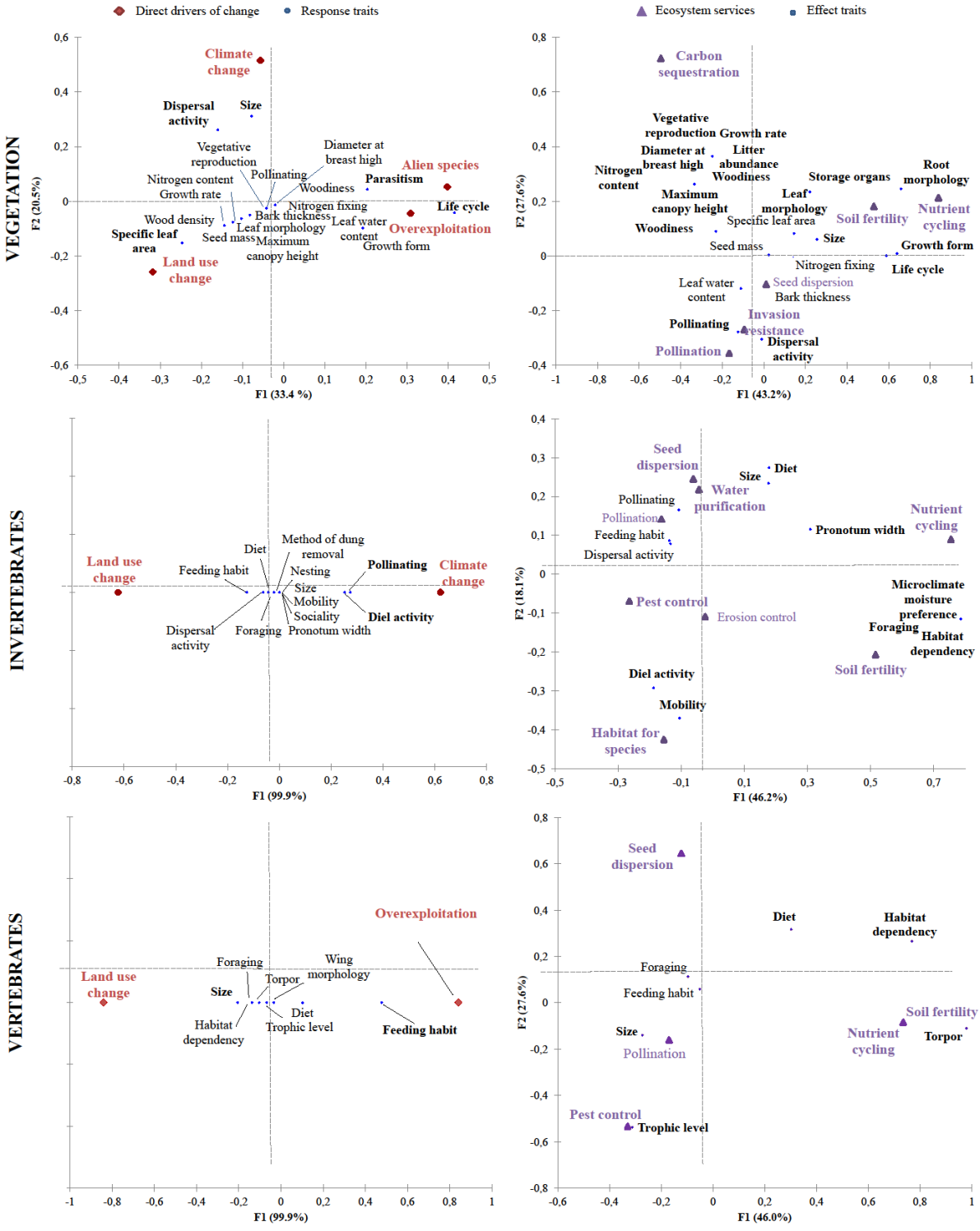

Figure 2.1.6. Biplots resulting from the RDA analyses performed for each taxonomic group to uncover the relationships between the direct drivers of change and response traits and between the effect traits and regulating services. Provisioning and cultural services are not used in this analysis as they were scarcely represented in our sample. Bold red text represents the direct drivers of change with higher standardised canonical coefficients and bold violet text represents

the ecosystem services with higher squared cosines for axes 1 and 2. Bold black font represents the response traits with higher squared cosines, while for the effect traits, bold black font represents the traits with higher standardised canonical coefficients.

2.1.4 Discussion

Our literature review documents existing evidence of links between the direct drivers of change and the supply of ecosystem services, mediated by the functional traits that modulate how species respond to drivers and how they affect ecosystem properties. We acknowledge that our results mostly reflect what has been studied to date, rather than the intensity and degree of those significant relationships. However, the evidence synthesized here may help improve our understanding about the linkages between the response of biodiversity to environmental change and biodiversity effects on ecosystem services, which is the missing link of the so called "holy grail" in functional ecology (Lavorel & Garnier 2002; Lavorel et al. 2007).

Gaps and biases in trait-based approaches to analyse links between drivers and ecosystem services

Our results on the historical trends in functional traits-ecosystem services investigation are consistent with previous studies that analysed the temporal evolution of general ecosystem services research in different ecoregions and at different geographical scales (Vihervaara et al. 2010; Nieto-Romero et al. 2014). However, in contrast to previous studies (Vihervaara et al. 2010), we found that trait-based research is clearly biased towards agroecosystems (mostly cultivated areas) and forest ecosystems, whereas studies on inland aquatic, coastal and marine systems remain limited. Our review also shows some biases in the geographical coverage of studies, with important gaps existing in the tropical regions of South America, Africa and Southeast Asia, which are essential for global biodiversity conservation (Myers et al. 2000). Most of the studies were conducted in Europe, which is coherent with the extended application of the ecosystem services approach in this region (Seppelt et al. 2011). This geographical bias is particularly relevant given that the influence of traits in ecosystem functioning and the provision of ecosystem services is highly context dependent (Hooper et al. 2005;

Srivastava & Vellend 2005; Abelleira-Martínez et al. 2016). Consequently, this bias largely hinders the global application of trait-based approaches at present.

Furthermore, this review showed a clear bias towards research conducted at local scales. The spatial scale of the analysis has a strong influence on the form of the relationship among land use change, functional traits and ecosystem services (Gross et al. 2000; Hevia et al. 2016). Consequently, it is important to address how the scale of land use activities affects functional traits and how this might affect the provision of ecosystem services at multiple scales (de Lima et al. 2013; Nagendra et al. 2013; Newbold et al. 2014; Gilroy et al. 2015).

Interestingly, few papers studied various groups of organisms simultaneously in the trait-based literature. To overcome this important gap, there have been recent calls for cross-taxon studies (Moretti et al. 2013) and for the use of functional metrics across trophic levels to develop more comprehensive biodiversity monitoring (Vandewalle et al. 2010; Lavorel et al. 2013; Hevia et al. 2016).

Most trait-based studies have focused on the effects of land use (see Fig. 4), which is coherent because land use change is the most important direct driver of biodiversity erosion at a global scale (Pereira et al. 2012). Thereby, it has received more scientific attention than any other driver of change in biodiversity conservation literature (Fazey et al. 2005; Velasco et al. 2015). In particular, recent studies have demonstrated how land use intensification is related to the loss of functional traits and erosion of multiple ecosystem services (Laliberté et al. 2010; Brown et al. 2013; García-Llorente et al. 2015).

Similar to what has been found for drivers of change, few studies have assessed more than one category of ecosystem services simultaneously. These findings are consistent with previous reviews showing that regulating services are the category receiving the greatest focus in ecological research (Harrison et al. 2014). This result may be explained by the evident direct link between regulating services and ecosystem functions, which is less distinct for other service categories (i.e. provisioning and cultural services) that are more dependent on social constructs (Daniel et al. 2012). Recent studies have also highlighted that functional traits more closely related with cultural ecosystem services are those that receive less attention (e.g. organism colour, birdsong, olfactory traits, etc.; Goodness et al. 2016). Therefore, additional studies are required to assess the potential

effects of drivers of change on cultural or provisioning services, via less-conventional functional traits.

Furthermore, most studies in this review only investigated one ecosystem service, which is consistent with previous reviews of ecosystem services research (Seppelt et al. 2011; Mitchell et al. 2013; Nieto-Romero et al. 2014). The fact that the functional traits literature has not addressed multiple ecosystem services largely hinders its potential application in landscape management, as this application necessarily requires uncovering ecosystem services trade-offs and synergies (i.e., negative and positive associations between ecosystem services, respectively) (Mouchet et al. 2014).

Searching for key functional traits linking drivers and ecosystem services

We found that some single functional traits (e.g. size or diet) may contribute to the provision of several ecosystem services, while responding to specific drivers of change (e.g. land use change and climate change; see Fig. 4). This indicates their potential role as "key functional traits", involved in the regulation of the system. "Keystone species" refer to specific system elements able to guarantee ecosystem functioning and the provision of multiple ecosystem services (Biggs et al. 2012). Thus, here we propose that specific functional traits that influence the provision of diverse ecosystem services and respond to drivers of change across a variety of systems and organisms might be considered as "key functional traits". In fact, these are traits that, if affected by a given driver of change, will have major consequences on ecosystem functioning. Therefore, it could be effective to focus environmental monitoring efforts on these traits, because of their potential effects on multiple ecosystem properties and services. Further, as some of these key functional traits (e.g. size) are relevant for different taxonomic groups, they might also be useful for incorporating cross-taxon and multi-trophic perspectives to this research topic (Lavorel 2013).

Establishing relationships among direct drivers of change, key functional traits and ecosystem services could lead to a major advance in ecological research (Lavorel & Garnier 2002). Our review suggests that an improved understanding about the key functional traits, associated with both the capacity to respond to environmental changes and the capacity to contribute to ecosystem properties, could help develop robust indicator systems to monitor changes in biodiversity and their effect on ecosystem

functioning and the delivery of ecosystem services. Some of the identified key functional traits are relatively easy to measure (e.g., size, leaf morphology), making them particularly useful for monitoring the effects of environmental change on ecosystem properties and the potential supply of ecosystem services. In this sense, the identification of the key functional traits can contribute to the further development of the Essential Biodiversity Variables (EBVs) (Pereira et al. 2013) within the EBV class of species-traits. Further, such knowledge might be also relevant for the global and regional biodiversity and ecosystem services assessments that have been recently launched by the Intergovernmental Platform of Biodiversity and Ecosystem Services (IPBES), because the trait-based approach shows the importance of particular traits for mediating between direct drivers of change and the supply of "nature's benefits to people" (Díaz et al. 2015). Thus, the present study could contribute to both initiatives, EBVs and IPBES, by providing a synthesis of evidence that has already been published.

To date, few studies have tested the overlap between response and effect traits that actually underlie the relationships between drivers and ecosystem services (but see Suding et al. 2008; Díaz et al. 2013). While more studies are certainly needed in this direction, our results provide indirect but novel evidence of this type of overlap. Our analyses suggest that most response traits that are strongly associated with specific direct drivers of change also act as effect traits. Although this is just a preliminary indication of the strength of the overlap between response and effect traits, our results suggest that the same traits studied in response to environmental change across a variety of systems and organisms may be involved in the control of ecosystem function and the supply of particular ecosystem services. This finding might have important implications for the resilience of ecosystems in the face of environmental change (Suding et al. 2008; Nimmo et al. 2015; Seidl et al. 2015) and, thereby, for the resilience of associated ecosystem services (Díaz et al. 2013; Biggs et al. 2012, 2015). The overlap between effect and response traits may lead to different resilience pathways in the community (Oliver et al. 2015). If there is a positive correlation between effect and response traits, a decline in the populations of species with those traits after a particular environmental perturbation may lead to a decline in the ecological properties fostered by particular effect traits that appear in such populations. For example, the trait of body size in female bees acts as a response trait under agricultural intensification, but also acts as an effect trait that contributes to pollination efficiency. This correlation between effect and

response traits may lead to a decline in the ecosystem service of pollination following agricultural intensification processes (Larsen et al. 2005).

In contrast, completely uncorrelated response and effect traits may guarantee the maintenance of ecological properties when the responses of species to environmental perturbations are decoupled from their effects on ecological processes (Díaz et al. 2013; Oliver et al. 2015). For example, Radchuk et al. (2015) found that insecticides in freshwater systems affect particular feeding guilds (response trait) of zooplankton (i.e. herbivores, carnivores and detritivores), but this does not destabilise the ecological processes of gross primary production and respiration. The main reason is that effect traits that seem to foster both ecological processes are different traits, such as body size and the feeding guild of omnivores. This example also pinpoints that the provision of ecosystem services often depends on the interactions between multiple traits across multiple trophic levels (Lavorel et al. 2013; Thompson et al. 2015).

Finally, an overlap between effect and response traits shows that species that have similar contributions to a particular ecological process may differ in their responses to disturbances and, thereby, might enhance the resilience of the system by increasing response diversity (Suding et al. 2008; Mori et al. 2013). For instance, seed dispersion in Uganda forests is performed by mammals with a diverse range of sizes, from mice to chimpanzees. Under localised disturbances, such as land use change, small mammals with low mobility are negatively affected, whereas more mobile and larger species maintain the seed dispersal function (Peterson et al. 1998). However, it is important to note that the overlap between effect and response traits is only one of the mechanisms that enhance the resilience of ecosystem services. Many other mechanisms have been identified in the literature, such as genetic variability, species diversity, species populations, landscape heterogeneity and landscape functional connectivity (Biggs et al. 2015; Nimmo et al. 2015; Oliver et al. 2015).

Future challenges and applications

Despite trait-based ecosystem services research having developed considerably over the last decade, our scientific understanding about the interlinkages among direct drivers of change and ecosystem services mediated by functional traits remains limited. Based on the biases found in our review, we propose here three major challenges for future

research: (a) expanding spatial scales and geographical coverage, (b) addressing complex relationships through cross-taxon, multi-trophic approaches and (c) addressing associations and interactions among functional traits.

First, despite recent advances, additional research is needed to fill current knowledge gaps, particularly with respect to several types of ecosystems, geographical coverage and the scale of analysis. For example, more research is needed to identify particular characteristics in the relationships among drivers, traits and ecosystem services in currently less studied ecosystems (e.g. inland aquatic, coastal and marine systems) and geographic regions (e.g. tropical areas). Moreover, although the trait-based approach has been validated at local scales (Lavorel et al. 2013), certain drivers of change (such as climate change) operate at much broader scales. Thus, the trait-based approach should also be applied beyond the local scale (Wood et al. 2015).

Second, although research within the last few years has begun to use a multi-trophic approach, by considering the interaction between vegetation traits and other organisms' traits (Grigulis et al. 2013; Lavorel et al. 2013; Moretti et al. 2013; Storkey et al. 2013), it is important to further characterise traits across taxonomic groups and trophic levels, as well as their interrelationships (Lavorel 2013; Violle et al. 2014; Wood et al. 2015). To develop these cross-taxon and multi-trophic trait-based approaches, it might be crucial to be able to use a shared code of traits. Furthermore, such cross-taxon comparison would require improving collaborative data sharing. This could be facilitated by the development of trait databases, such as TRY (http://www.try-db.org/, Kattge et al. 2011) and TraitNet (http://raitnet.ecoinformatics.org/) that have been developed for plants at a global scale. Trait databases also exist for animals at a regional scale, including vertebrates (i.e. fish; Frimpong & Argemeier 2009) and invertebrates, such as ground beetles (Homburg et al. 2014), cavity-nesting wasps and bees (Scales project; http://www.scales-project.net/), hoverflies (Speight et al. 2013) and aquatic macroinvertebrates (Vieira et al. 2006; Statzner et al. 2008). However, for most taxonomic groups of invertebrates and vertebrates, available trait databases are still missing (Gossner et al. 2015).

Finally, we found that most functional traits that are responsible for the response of species to various direct drivers of change (response traits) are also traits that affect ecosystem services supply (effect traits). The multivariate analyses allowed us to identify some key functional traits, which were delineated as those that have the

potential capacity to provide multiple ecosystem services while responding to specific drivers of change. Future research to consolidate a list of traits (and bundles of traits) that are able to respond to drivers of change, while maintaining the provision of ecosystem services, would be highly relevant to design and apply robust environmental policies that ensure the conservation of these 'key functional traits' and, thereby, preserve the resilience of ecosystems.

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Appendix S1. List of all of the keywords used in the systematic review:

Direct Drivers of Change

"Abandonment" or "Acid rain" or "Acidification" or "Alien species" or "Carbon cycle" or "Clima* change" or "Desertification" or "Exotic species" or "Fragmentation" or "Global warning" or "Habitat change" or "Habitat conversion" or "IAS" or "Intensification" or "Intensive agriculture" or "Invasive species" or "Invasive-alien species" or "Land conversion" or "Land cover and change" or "Land degradation" or "Land use conversion" or "Land-use change" or "Land-use intensity" or "Nitrogen cycle" or "Non-native species" or "Overexploitation" or "Overharvesting" or "Overuse" or "Phosphorous cycle" or "Pollution" or "Sulfure cycle" or "Sulphur cycle" or "Urbanization"

AND

Functional Diversity

"Functional richness" or "Functional character*" or "Functional composition" or "Community weight*" or "Functional effect*" or "Functional divergence" or "Functional trait*" or "Dominant trait*" or "Organism providing servic*" or "Functional diversity" or "Service provid* unit" or "Trait effect*" or "Ecological attribute*" or "Ecosystem service provid*" or "Trait range*" or "Trait reponse or response trait" or "Functional group*" or "Effect trait*" or "Functional guild*" or "Functional dispers*" or "Functional redundancy" or "Functional respon*" or “Agregate trait mean” or “Niche complementary” or “growth form*” or “SPU” or “Trait dissimilarit*” or “mass ratio” or “CWM”

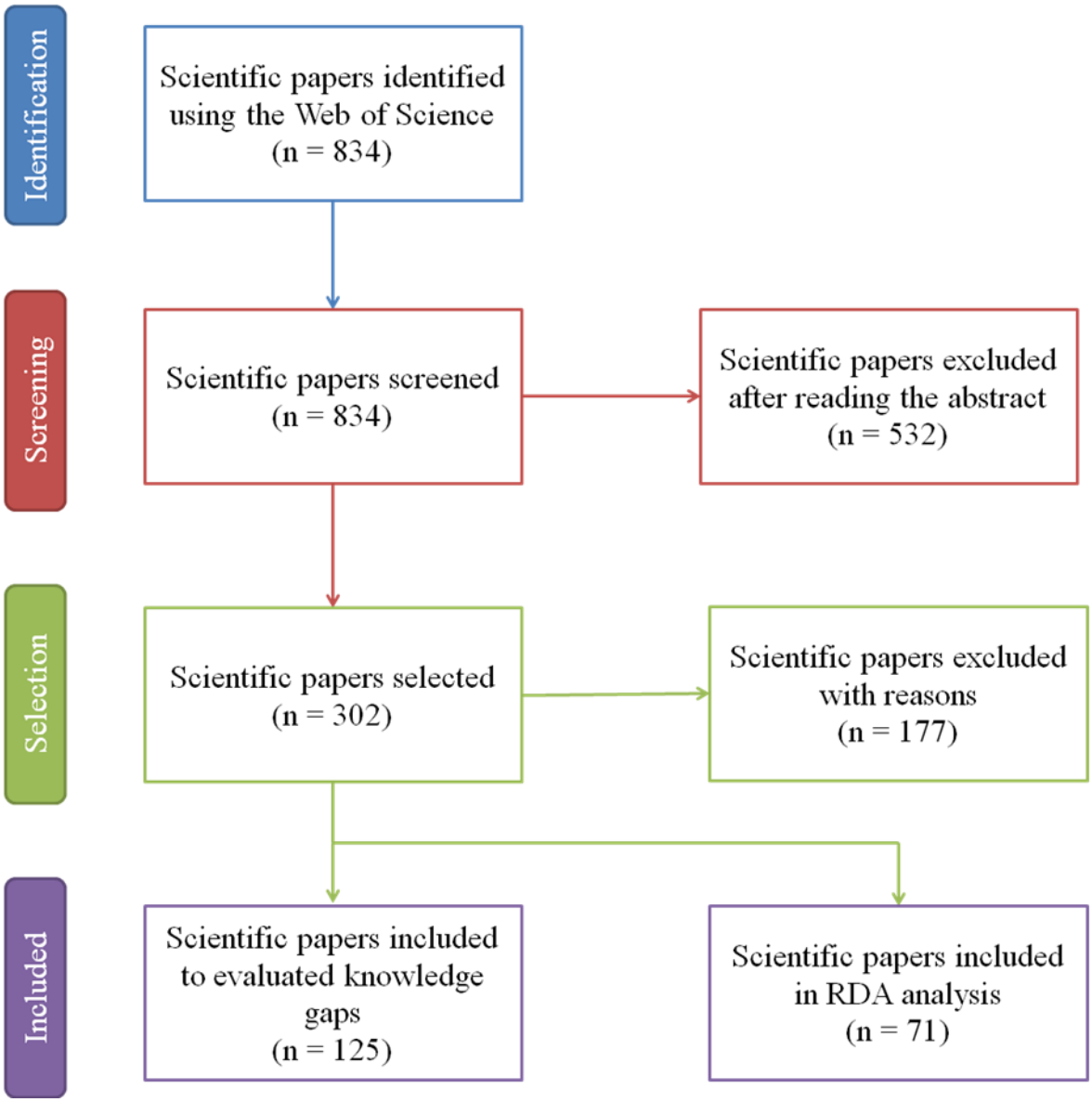
AND

Ecosystem services

"Ornamental resources" or "Fodder" or "Habitat provision" or "Eco* good*" or "Wild prod*" or "Timber" or "Biofuels" or "Ecosystem* servic*" or "Regulating servic*" or "Nontimber forest" or "Air flow regulation" or "Habitat maintenance" or "Habitat for species" or "Biological control" or "Air quality" or "Provisioning servic*" or "Fiber" or "Erosion control" or "Atmospheric regulation" or "Biocontrol" or "Hazard prevention" or "Bioremediation" or "Carbon sequestration" or "Water quality" or "Fibre" or "Carbon storage" or "Erosion prevent" or "Climate regulation" or "Raw material*" or "Agriculture" or “Livestock” or “Cattle” or "Genetic resources" or "Medicinal resources" or "Disease control" or "Hydrological regulation" or "Invasion resistance" or "Nutrient cycling" or "Pest control" or "Plague control" or "Plague prevention" or "Pollination" or "Sediment retention" or "Seed dispers*" or "Soil fertility" or "Soil formation" or "Soil loss prevention" or "Soil stability" or "Waste treatment" or "Water

purification" or "Water regulation" or "Cultural servic*" or "Aesthetic values" or "Cultural heritage" or "Cultural value*" or "Ecological knowledge" or "Environmental education" or "Fishing*" or "Hunting*" or "Identity" or "Inspiration" or "Landscape beauty" or "Recreat*" or "Relax*" or "Sacred places" or "Scientific knowledge" or "Scientific value*" or "Sense of place" or "Spiritual" or "Touris*" or "Tranquility" or "Turis*".

Appendix S2. Scientific literature search flow diagram.



Appendix S3. List of papers considered in the review.

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Appendix S4. List of variables considered and the corresponding attributes.

Variables	Attributes
Publication characteristics	
Number of authors	
Category of Web of Science	Ecology, Botany, Biodiversity and Conservation, Hydrobiology, Zoology, Environmental Sciences, Others
Interdisciplinary team	Yes, No
Year of publication	
Journal	
Research area	
Type of study	Experimental, Observational, Predictive
Location	
Location of the study area	
Methodological approach	
System border definition	Administrative, Biophysical
Spatial scale	Global, Regional, National, Subnational, Local
Taxonomic group	Invertebrates, Vegetation, Vertebrates
Period of study	Monitoring, Punctual
Characteristics of ecosystems	
Type of ecosystem (based on Millennium Ecosystem Assessment)	Coastal, Cultivated, Dryland, Forest, Inland water, Marine, Polar, Urban, Interaction
Protected area	Yes, No
Direct Drivers of change	
Type of Direct Drivers of change	Pollution, Alien species, Climate change, Land use change, Overexploitation
Functional Traits	
Functional traits used in the study	
Ecosystem services	
Type of ecosystem services	Cultural, Provisioning, Regulating
Statistical relation	
Driver-Functional diversity	Positive, Negative, Not significant
Functional diversity-Ecosystem services	Positive, Negative, Not significant
Driver-Ecosystem services	Positive, Negative, Not significant

Appendix S5. List of the functional traits for each taxonomic group recorded in our literature sampling. The last column shows the number of studies which used each functional trait.

Functional trait	**Taxonomic group**			**Nº of studies**
	Vegetation	Invertebrates	Vertebrates	
Allometries		✓		1
Bark thickness	✓			1
Bill length			✓	1
Breeding season		✓		2
C:N ratio	✓			1
Canopy structure	✓			2
Carbon content	✓			2
Clutch size			✓	1
Cold tolerance			✓	1
Consumption			✓	2
Diameter at breast height	✓		✓	
Diel activity		✓		5
Diet		✓	✓	24
Dispersal activity	✓	✓	✓	20
Dry matter content	✓			4
Duration of flower visitation		✓		1
Feeding habit		✓	✓	16
Flocking behaviour			✓	1
Flower color	✓			1
Foraging		✓	✓	6
Generation length			✓	2
Growth form	✓			20
Growth rate	✓			2
Habitat dependency	✓	✓	✓	21
Leaf morphology	✓			6
Leaf physiology	✓			1
Leaf water content	✓			1
Life cycle	✓			13
Litter abundance	✓			5
Mating strategy			✓	1
Maximum canopy height	✓			7
Method of dung removal		✓		1
Microclimate moisture preference		✓		2
Migration			✓	3
Mobility		✓	✓	3
Nectar and pollen production	✓			1
Nesting			✓	3
Nitrogen content	✓			3
Nitrogen fixing	✓			5
Nº of visited flowers		✓		1

Functional trait	**Taxonomic group**			**Nº of studies**
	Vegetation	Invertebrates	Vertebrates	
Number of cotyledons	✓			1
Nutrient mineralisation	✓			1
Onset and/or duration of flowering	✓			3
Overwintering stage		✓		3
Parasitism		✓		3
Phenology	✓			2
Photosynthesis traits	✓			2
Pollen distribution		✓		1
Pollinating	✓	✓		5
Proboscis morphology		✓		2
Production	✓			3
Pronotum width		✓		1
Recruitment			✓	1
Reproductive effort	✓			3
Reproductive success	✓			1
Root morphology	✓			2
Root physiology	✓			1
Root:shoot ratio	✓			1
Seed mass	✓			10
Seed number	✓			1
Self-compatibily	✓			1
Shade tolerance		✓		1
Size	✓	✓	✓	37
Social organisation		✓		2
Sociality		✓		1
Specific leaf area	✓			16
Storage organs	✓			1
Tongue length		✓		1
Torpor			✓	1
Trophic level		✓	✓	12
Vegetative reproduction	✓			3
Vertical distribution	✓			1
Wing morphology			✓	1
Wood density	✓			3
Woodiness	✓			4

Appendix S6. Scores for the redundancy analysis (RDA) variables and statistics. Bold values represent those response traits (dependent variables) and those explanatory variables with scores > 0.2.

❖ **Vegetation group**

	Axis1	Axis2	Axis3
Dependent variables (response traits)			
Nitrogen fixing	-0,041	-0,025	0,008
Size	-0,078	**0,312**	-0,035
Dispersal activity	-0,160	**0,261**	-0,019
Life cycle	**0,415**	-0,041	0,032
Seed mass	-0,144	-0,088	0,028
Specific leaf area	**-0,247**	-0,152	0,048
Parasitism	**0,203**	0,044	0,272
Pollinating	-0,021	-0,013	0,004
Leaf morphology	-0,123	-0,076	0,024
Growth form	0,191	-0,098	-0,236
Maximum canopy height	-0,144	-0,088	0,028
Woodiness	-0,041	-0,025	0,008
Vegetative reproduction	-0,041	-0,025	0,008
Growth rate	-0,041	-0,025	0,008

Nitrogen content	-0,041	-0,025	0,008
Wood density	-0,103	-0,063	0,020
Bark thickness	-0,082	-0,051	0,016
Leaf water content	-0,082	-0,051	0,016
Diameter at breast high	-0,021	-0,013	0,004
Explanatory variables (direct drivers)			
Alien species	**0,398**	0,053	0,090
Climate change	-0,056	**0,515**	-0,063
Land use change	**-0,318**	-0,258	0,300
Overexploitation	**0,308**	-0,044	-0,258
Eigenvalue	0,620	0,380	0,204
Percentage variance explained	33,451	20,490	11,022
Cumulative % variance explained	33,451	53,941	64,963
Total inertia	30,110	18,443	9,921

- **Invertebrates group**

	Axis1
Dependent variables (response traits)	

Size	0,000
Feeding habit	-0,126
Diel activity	**0,252**
Dispersal activity	-0,063
Mobility	-0,021
Foraging	-0,042
Diet	-0,063
Nesting	-0,021
Sociality	-0,021
Pollinating	**0,273**
Pronotum width	-0,021
Method of dung removal	-0,021
Explanatory variables (direct drivers)	
Climate change	**0,622**
Land use change	**-0,622**
Eigenvalue	0,031
Percentage variance explained	100,000
Cumulative % variance explained	100,000
Total inertia	3,091

❖ **Vertebrates group**

	Axis1
Dependent variables (response traits)	
Size	**-0,205**
Feeding habit	**0,478**
Foraging	-0,137
Diet	0,102
Trophic level	-0,068
Habitat dependency	-0,102
Wing morphology	-0,034
Torpor	-0,068
Explanatory variables (direct drivers)	
Land use change	**-0,841**
Overexploitation	**0,841**
Eigenvalue	0,094
Percentage variance explained	100,000
Cumulative % variance explained	100,000

Total inertia	7,857

Appendix S7. Scores for the redundancy analysis variables and statistics. Bold values represent those ecosystem services (dependent variables) and those explanatory variables with scores > 0.2

❖ **Vegetation group**

	Axis1	Axis2	Axis3
Dependent variables (ecosystem services)			
Invasion resistance	-0,094	**-0,268**	-0,081
Pollination	-0,167	**-0,356**	0,354
Nutrient cycling	**0,840**	**0,213**	-0,150
Seed dispersion	0,011	-0,103	-0,283
Soil fertility	**0,529**	0,181	0,388
Carbon cycling	**-0,495**	**0,723**	0,050
Explanatory variables (effect traits)			
Litter abundance	**-0,248**	**0,365**	0,022
Nitrogen fixing	0,141	-0,003	-0,163
Size	**0,256**	0,061	-0,194
Dispersal activity	-0,012	**-0,304**	-0,162
Life cycle	**0,590**	0,001	0,297
Seed mass	0,025	0,004	-0,535
Specific leaf area	0,145	0,083	-0,259

Pollinating	-0,124	**-0,277**	0,349
Leaf morphology	**0,222**	**0,234**	0,173
Growth form	**0,642**	0,009	0,043
Root morphology	**0,659**	**0,245**	0,324
Maximum canopy height	**-0,335**	**0,263**	-0,026
Woodiness	**-0,248**	**0,365**	0,022
Vegetative reproduction	**-0,248**	**0,365**	0,022
Growth rate	**-0,248**	**0,365**	0,022
Nitrogen content	**-0,248**	**0,365**	0,022
Wood density	**-0,232**	0,091	-0,040
Bark thickness	-0,111	-0,118	-0,058
Leaf water content	-0,111	-0,118	-0,058
Diameter at breast high	**-0,248**	**0,365**	0,022
Storage organs	**0,659**	**0,245**	0,324
Eigenvalue	0,107	0,066	0,033
Percentage variance explained	46,661	29,035	14,543
Cumulative % variance explained	46,661	75,697	90,239
Total inertia	13,977	8,698	4,356

❖ **Invertebrates group**

	Axis1	Axis2	Axis3
Dependent variables (ecosystem services)			
Habitat for species	-0,155	**-0,425**	-0,194
Erosion control	-0,024	-0,109	-0,030
Water purification	-0,044	**0,218**	-0,121
Pest control	**-0,265**	-0,069	**0,334**
Pollination	-0,163	0,142	**0,255**
Nutrient cycling	**0,755**	0,089	0,027
Seed dispersion	-0,062	**0,245**	**-0,206**
Soil fertility	**0,516**	**-0,207**	0,117
Explanatory variables (effect traits)			
Size	0,176	**0,234**	0,124
Feeding habit	-0,138	0,086	**-0,373**
Diel activity	-0,188	**-0,293**	0,032
Dispersal activity	-0,134	0,078	**-0,392**
Mobility	-0,105	**-0,371**	**-0,236**
Foraging	**0,786**	-0,115	0,137

Diet	0,178	**0,274**	-0,194
Habitat dependency	**0,786**	-0,115	0,137
Microclimate moisture preference	**0,786**	-0,115	0,137
Pollinating	-0,109	0,166	**0,202**
Pronotum width	**0,309**	0,116	-0,020
Eigenvalue	0,153	0,132	0,095
Percentage variance explained	30,455	26,237	18,965
Cumulative % variance explained	30,455	56,692	75,657
Total inertia	16,664	14,356	10,377

❖ **Vertebrates group**

	Axis1	Axis2	Axis3
Dependent variables (ecosystem services)			
Pest control	**-0,330**	**-0,533**	**0,406**
Pollination	-0,169	-0,161	**-0,483**
Nutrient cycling	**0,735**	-0,084	0,055
Seed dispersion	-0,123	**0,645**	**0,230**
Soil fertility	**0,735**	-0,084	0,055

Explanatory variables (effect traits)			
Size	**-0,273**	-0,140	**-0,245**
Feeding habit	-0,051	0,059	-0,074
Foraging	-0,097	0,112	-0,140
Diet	**0,302**	**0,317**	**0,504**
Trophic level	**-0,312**	**-0,538**	**0,508**
Habitat dependency	**0,769**	**0,267**	0,152
Torpor	**0,979**	-0,110	0,057
Eigenvalue	0,309	0,186	0,115
Percentage variance explained	45,982	27,626	17,041
Cumulative % variance explained	45,982	73,607	90,648
Total inertia	40,916	24,582	15,163

Capítulo 2.2

Efectos del uso del suelo sobre la diversidad taxonómica y funcional: un análisis multi-taxón en un paisaje mediterráneo

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2.2 Effects of land use on taxonomic and functional diversity: a cross‐taxon analysis in a Mediterranean landscape

Abstract

Land-use change is the major driver of biodiversity loss. However, taxonomic diversity (TD) and functional diversity (FD) might respond differently to land-use change, and this response might also vary depending on the biotic group being analysed. In this study, we compare the TD and FD of four biotic groups (ants, birds, herbaceous, woody vegetation) among four land-use types that represent a gradient of land-use intensity in a Mediterranean landscape (Mediterranean shrublands, dehesas, mixed-pine forests, olive groves). Analyses were performed separately at two different spatial scales: the sampling unit scale and the site scale. Land-use intensity effects on TD and FD were quite different and highly varied among the four biotic groups, with no single clear pattern emerging that could be considered general for all organisms. Additive partitioning of species diversity revealed clear contrasting patterns between TD and FD in the percentage of variability observed at each spatial scale. While most variability in TD was found at the larger scales, irregardless of organism group and land-use type, most variability in FD was found at the smallest scale, indicating that species turnover among communities is much greater than functional trait turnover. Finally, we found that TD and FD did not vary consistently, but rather followed different trajectories that largely depended on the biotic group and the intensity of land-use transformation. Our results highlight that the relationship of land use with TD and FD is highly complex and context-dependent.

Keywords: Biodiversity, Diversity partitioning, Functional traits, Land-use intensity, Spatial scale

2.2.1 Introduction

Land-use change is the most important direct driver of biodiversity loss at a global scale (Pereira et al. 2012) and has the additional large capacity to modify ecosystem functioning (Hector et al. 2001) and the provision of ecosystem services (Díaz et al. 2007; Nagendra et al. 2013; Allan et al. 2015). Most of the literature exploring the relationship between land-use change and biodiversity loss has focused on taxonomic diversity (TD) (Milder et al. 2008), with other components of biodiversity, such as functional diversity (FD), receiving less attention (Feld et al. 2009). FD is the value and range of functional traits of organisms present in a given ecosystem (Díaz and Cabido 2001), and a thorough understanding of FD is critical for addressing ecological questions (Mouillot et al. 2005; Mason and de Bello 2013).

Although researchers are showing an increasing interest in the study of FD and its dependence on environmental conditions (Mayfield et al. 2010), relatively few studies have linked FD responses with changes in land use. It has been shown that intensification processes tend to reduce FD, but the results of such studies are highly dependent on the site and the taxonomic group being studied (Flynn et al. 2009). Otherwise, it is highly uncertain whether changes in TD associated with land use are mirrored by changes in FD (Mayfield et al. 2010; Carmona et al. 2012). As TD and FD responses might differ, exploring their relationship will provide a more complete picture of the potential consequences of land-use change (Mayfield et al. 2010).

Scientific literature exploring FD has been historically biased towards certain taxonomic groups. Most of the studies published to date have focused on vegetation and invertebrates (i.e., insects) at local scales, with vertebrates being the least studied group (Hevia et al., under review). The response of functional traits to land-use change or other drivers of change may vary across different organism groups, depending, for example, on their home range, degree of mobility and size. Consequently, site-based studies applying the trait-based approach simultaneously to several taxonomic groups and trophic levels might be one approach to properly address the effects of drivers of change on FD. Recent research has begun to use this multitrophic approach (Moretti et al. 2013), seeking to combine taxonomic and functional indicators across trophic levels to develop more comprehensive biodiversity monitoring (Vandewalle et al. 2010).

In addition, a multi-scale perspective is necessary to improve our understanding of the effect of land-use change on species diversity and traits (Gilroy et al. 2015). The spatial

scale of analysis can highly influence the form of the relationship between diversity and ecosystem processes (Gross et al. 2000; Symstad et al. 2003). Consequently, there is a need to address the scale effects of land-use activities on biotic communities and to explore potential differences among groups of organisms (de Lima et al. 2013).

In the study reported here, we compared the TD and FD of four different biotic groups (ants, birds, herbaceous vegetation, woody vegetation) among four land-use types (Mediterranean shrublands, dehesas, mixed-pine forests, olive groves) that represent a gradient of land-use intensity in the Mediterranean landscape. We tested: (1) how different biotic groups respond to land-use type, (2) how the spatial scale of analysis (sampling unit vs. sampling site) provides different information about the potential effects of land-use change on biodiversity and (3) whether changes in TD and FD follow similar patterns of change along the intensity gradient.

2.2.2 Materials and methods

Study area

The study site is the upper watershed of the Guarrizas River (tributary of the Guadalquivir River), which is located in Eastern Sierra Morena (Jaén, Spain) [see Appendix A]. The area covers 28,123 ha and includes five municipalities: Aldeaquemada, Santa Elena, Vilches, Navas de San Juan and Santisteban del Puerto. The area is characterised by a continental Mediterranean climate, with mean annual precipitation of 700 mm and mean annual temperature of 15 °C. The study year was slightly wet, with rainfall exceeding the long-term mean precipitation for Jaén province by approximately 25 %, although it was within the typical variability range for this climate (AEMET 2012). The elevation of the study site ranges from 700 to 950 m a.s.l., and the lithology is mainly quartzite, slate and sandstone.

Four dominant land-use types occupy over 60 % of the study area: Mediterranean shrublands, dehesas, mixedpine forests and olive groves (see Appendix B). Mediterranean shrublands represent the natural vegetation of the study area, which mainly consists of holm oaks (*Quercus ilex*) and shrub and bush formations. These areas are usually managed for conservation purposes combined, in a number of privately owned lands, with tourism or game hunting. *Dehesas* are Mediterranean

agrosilvopastoral ecosystems and represent the first—and least intense–degree of land-use transformation. These systems consist of pasturelands with scattered trees (primarily holm oaks), which are mostly managed for extensive pastoralism with cattle, sheep and goats. Rearing of fighting bulls is also common in the dehesas of the study area. Mixed-pine forests (mainly Pinus pinaster, but with several other species of coniferous trees also present) represent a more intense degree of land-use transformation, primarily due to plantation programmes developed in the 1960s. Current management practices in these areas have the combined aim to thin the pine forests, extracting pine wood, and to promote recolonisation of native Mediterranean woody species (e.g., *Q. ilex, Q. faginea, Q. coccifera, Arbutus unedo*). Finally, olive groves are intensively managed for olive oil production and represent the most intense land-use transformation in the study area. Management practices in olive groves include periodic fumigation and, occasionally, soil tilling.

Sampling design and data collection

We selected 20 sampling sites (5 in each land-use type) for birds, herbaceous and woody vegetation, and 40 sampling sites (10 per land-use type) for ants. All sampling sites shared the same slope and orientation. We used different transects to sample the studied organisms, with the starting point of each transect randomly placed in each site. Sampling was conducted in May 2012.

Herbaceous vegetation

A 100-m-long transect was placed in each of the sampling sites, and ten 20 × 20-cm sampling units were regularly distributed along this transect. We identified all of the species present within the quadrat and estimated their coverage using the following categories: (1) <12.5 %; (2) 12.5–25 %; (3) 26–50 %; (4) 51–75 %; (5) >75 %. Based on a full list of species present at the site, we subsequently added a sixth category: (0) absent. Each species was then characterised according to three quantitative traits and six qualitative traits (Table 2.2.1) which have been reported to be relevant for dispersion, establishment and persistence (Weiher et al. 1999). Canopy height (defined as the distance between the highest photosynthetic leaf and the plant's base) was measured

following the guidelines provided by Cornelissen et al. (2003), specific leaf area (SLA) measurements were obtained from the TRY database (Kattge et al. 2011), and seed mass measurements were obtained from the SID database (Royal Botanic Gardens Kew 2015). Data on qualitative traits were obtained from Blanca et al. (2009) and Castroviejo (2009).

Biotic group	Trait[a]	Range / categories
Herbaceous plants	SLA	7.66 - 56.34 mm^2/mg
	Seed mass	0.016 - 83.7 mg
	Canopy height	4- 250 cm
	Start of flowering	1 – 9 month (January to September)
	Growth form	Graminoid; Prostrate; Erect; Rosette
	Defensive structures	Yes; No
	Dispersive structures	Yes; No
	Clonability	Yes; No
	Legume	Yes; No
Woody plants	SLA	2.40 - 28.62 mm^2/mg
	Seed mass	0.047 - 718.0 mg
	Canopy height	0.1 - 4.5 m
	Dispersal	Autochory; Animals; Wind
	Defensive structures	Yes; No
	Life form	Phanerophyte; Chamaephyte; Terophyte
Ants	Eye length	0.027 - 0.4786 mm
	Femur length	0.060 - 3.041 mm
	Diet	Aphids; Predator; Grains; Nectar; Carrion
	Functional group[b]	HCS/OH; C; CCS/SH; GO
Birds	Bill length relative to	0.037 - 2.157 mm/g

weight	
Clutch size (mean)	2 - 13
Nest location	Ground, Tree holes; Buildings; Trees; Parasite
Foraging location	Foliage; Canopy; Ground; Litter; Trunk; Bark; Flying
Diet	Insects; Seeds; Leaves; Small vertebrates; Fruits; Omnivorous

SLA, Specific leaf area

[a] Several other traits (tibia length and head width for ants; bill type, wing, tarsus and tail length relative to weight for birds) were also measured but were not included in the analyses as they showed significant correlations with a number of the selected traits

[b] Ant functional groups were cold-climate specialists and/or shade habitats (CCS/SH); cryptic (C); generalists and/or opportunistic (GO); hot climate specialists and/or open habitats (HCS/OH)

Table 2.2.1 List of the functional traits for each organism group included in the analyses.

Woody vegetation

Each of the sampling sites consisted of a 1 km-long transect. Ten 10 × 10-m sampling units were regularly distributed along this transect. We identified all of the woody species present within the plot and estimated their coverage using the same scale used for herbaceous vegetation. Each species was then characterised according to three quantitative traits and three qualitative traits (Table 2.2.1) that have been reported to be relevant for dispersion, establishment and persistence (McIntyre et al. 2007). Life form was characterised according to the Raunkiaer system for classification of life form. Canopy height was measured in situ, SLA measurements were obtained from the TRY database (Kattge et al. 2011), and seed mass measurement were obtained from the SID database (Royal Botanic Gardens Kew 2015). Data on the remaining traits were obtained from Blanca et al. (2009), Castroviejo (2009) and Ruiz de la Torre (2006).

Ants

Each sampling site consisted of a 50-m-long transect where one pitfall trap was placed systematically every 10 m, accounting for a total of five pitfall traps per sampling site. Traps were 2 cm in diameter and 5 cm deep and contained a mixture of 70 % ethanol and 30 % monoethylene glycol. Pitfall traps were left in the field for 7 days. Despite some limitations to this capture approach, pitfall traps are considered to be the most objective and fastest method to sample ground-dwelling ants (Nash et al. 2004).

Ants were identified to the species level with a binocular microscope and were then characterised according to four quantitative and two qualitative functional traits (Table 2.2.1). The selection of these traits was based on important characteristics recognised in ant ecology (Azcárate et al. 2013). We measured eye length, head width, tibia length and femur length in a sample size of ten individuals per species randomly selected from the whole sample. Qualitative traits were obtained from Azcárate and Peco (2012) and Hevia et al. (2013). Specifically, to classify species into functional groups (i.e. groups of species that respond to disturbance in a similar manner), we followed the classification of Roig and Espadaler (2010), who delineated eight categories: invasive and/or exotic, generalists and/or opportunistic, social parasites, specialist predators, coarse woody debris specialists, cold-climate specialists and/or shade habitats, hot climate specialists and/or open habitats and cryptic.

Birds

In each sampling unit, the bird community was surveyed by means of five point counts separated by 200 m and located along a randomly selected 1-km linear transect. All counts were performed in the early morning (2 h after sunrise) or late afternoon (2 h before sunset), avoiding rainy or windy days. We spent 5 min on each point count, recording every bird heard or seen within a 50-m radius (birds overflying the plot were not included).

We selected five quantitative and four qualitative functional traits (Table 2.2.1), based on bird traits linked to ecosystem response to disturbance (Petchey and Gaston 2006). Quantitative traits were obtained from the National Ringing Database of the Spanish Ornithological Society and only birds ringed in the Eastern Sierra Morena area were selected for the analysis. Qualitative traits were obtained from the published literature (Cramp and Perrins 1994).

TD and FD calculation

Quantitative traits were log-transformed as needed to attain a normal distribution of trait values. Qualitative traits were split into binary traits which allowed a species to be classified into more than one group. The month in which flowering started was considered to be a circular trait (e.g., the correct dissimilarity between one species flowering in January and one flowering in December is 1 month; Leps et al. 2006). For each trait of each biotic group, we calculated a matrix of dissimilarities among species using Gower distances. We subsequently performed Mantel tests (9999 permutations) between the respective matrices of trait distances between species and discarded traits that yielded significant correlations with other traits to avoid redundant information. With the final set of traits for each biotic group (Table 2.2.1), we calculated a matrix of pairwise functional dissimilarities (using Gower distances) between species considering multiple traits. In this calculation, the functional dissimilarity between any two species varies between 0 (when the traits of two species are identical) and 1 (when two species are completely dissimilar).

For each biotic group, we considered two different spatial scales: (1) the sampling unit scale, which represented the smallest unit of collected information for that biotic group (e.g. 20 × 20-cm quadrats for herbaceous plants, or pitfall traps for ants) and (2) the site scale, which was composed of a number of sampling units placed at the same spatial location (e.g. the 10 quadrats or the 5 pitfall traps placed on a given *dehesa* grassland). To calculate the relative abundance of documented species at the site scale, we averaged their coverage in the sampling units (in the case of plants) or calculated the proportion of sampling units in which each species was present (in the case of ants and birds).

We calculated the FD of each biotic group using the Rao index:

$$Rao = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij}\, p_i p_j$$

where d_{ij} is the dissimilarity in trait values between each pair of coexisting species *i* and *j*, while p_i and p_j indicate the relative abundances of species *i* and *j*, respectively, in the community under consideration (Ricotta and Moretti 2011). In addition, we calculated the Simpson index of diversity:

$$Simpson\ index = 1 - \sum_{i=1}^{S} p_i^2$$

The Simpson index of diversity is equivalent to the Rao index when all the dissimilarities between species are equal to 1 (Leps et al. 2006). Finally, we expressed both TD and FD in terms of equivalent numbers (de Bello et al. 2010). The hierarchical nature of our sampling design (sampling units within sites), along with the combined use of the Rao and Simpson indices, provided a common framework to study the partitioning of both TD and FD across spatial scales (de Bello et al. 2010; Carmona et al. 2012).

We studied the changes in diversity across spatial scales and land-use types using two complementary analyses. First, we calculated FD and TD at the two spatial scales considered (diversity within sampling units and diversity within sites) using the relative abundance of each species at each scale to calculate the Rao index and the Simpson index of diversity. In addition, for each of the considered land-use types and biotic groups, we performed a partition of diversity at different spatial scales. Following de Bello et al. (2010), we first calculated α-diversity (within sampling units) and γ-diversity (total diversity, calculated by pooling all of the sampling units of all the sites). This information allowed us to calculate β-diversity, which is the difference between γ-diversity and the average of the α-diversity of the sampling units and expresses the proportion of diversity that occurs due to differences between sampling units.

Subsequently, we repeated this process, but considered site as the level at which α-diversity is calculated (de Bello et al. 2010). In this second case, β-diversity represents the proportion of diversity that is found between the sites considered in the whole study area. Therefore, for each land-use type and biotic group, we partitioned TD and FD at three hierarchical levels: within sampling units, within sites and between sites (Carmona et al. 2012).

Data analysis

The differences in TD and FD between land-use types were examined at the two considered spatial scales (sampling unit and site) for all of the biotic groups under

consideration. Using linear mixed models, we first examined the effect of land-use type on diversity at the sampling unit scale, with site as a random-effects factor to account for the lack of independence of sampling units within sites and the type of land use as a fixed-effects factor. Whenever we found a significant ($P < 0.05$) effect of land-use type on the considered diversity index, we used the R add-on package multcomp to perform a Tukey post hoc test to detect any differences between individual land-use types.

We also analysed the differences in diversity between land-use types at the site scale by performing analyses of variance, in which we used land use as the explanatory variable. Similarly, we performed a Tukey HSD post hoc test for cases where land use had a significant effect. All of these analyses, as well as the partitioning of diversity described in this section, were performed using the R data analysis software (v.3.1.1.; Team R Core 2014).

2.2.3 Results

Effects on taxonomic and functional diversity across scales and biotic groups

Herbaceous plant diversity

A total of 117 herbaceous species were recorded during sampling, of which 50 species were recorded in Mediterranean shrublands, 83 in dehesas, nine in mixed-pine forests and five in olive groves (see Appendix C, Table 2.2.1).

At the sampling unit scale, TD differed among the four land-use types ($F = 38.56$; $P < 0.0001$), being significantly higher in dehesas than in the other three land-use types which in turn did not significantly differ from each other (Fig. 2.2.1). We also found significant differences among land-use types for FD ($F = 37.73$; $P < 0.0001$), with the highest and lowest values being obtained in dehesas and olive groves, respectively (Fig. 2.2.1). The TD and FD values of Mediterranean shrublands and mixed-pine forests did not differ significantly.

At the site scale, TD differed among land-use types ($F = 10.93$; $P = 0.0009$). Specifically, TD was significantly higher in dehesas than in all other land-use types, which in turn did not significantly differ from each other (Fig. 2.2.1). This result

contrasted with that obtained for FD, where only olive groves (with extremely low FD values) differed from the other land-use types (Fig. 2.2.1).

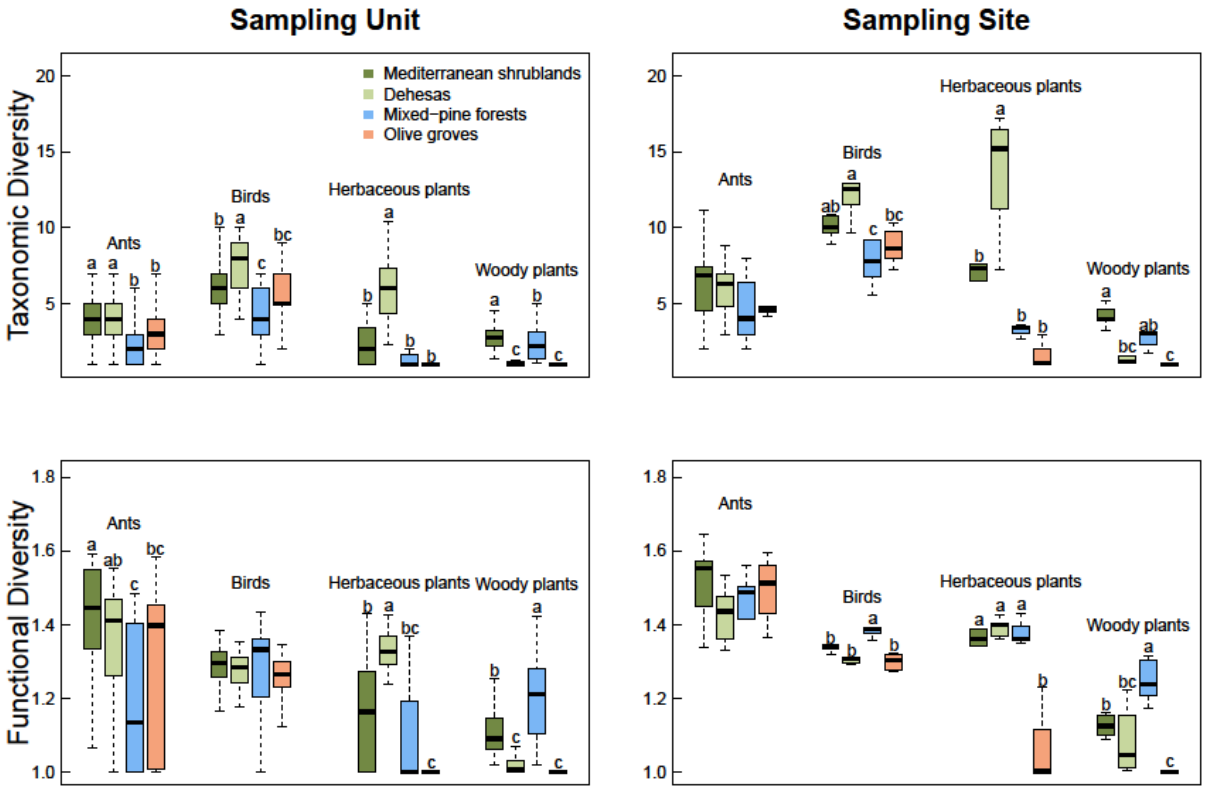

Fig. 2.2.1 *Boxplots* showing the effect of land-use type on taxonomic diversity (TD; Simpson's index) (a, b) and functional diversity (FD; Rao index) (c, d) for the four biotic groups at the sampling unit (a, b) and sampling site (c, d) scale. Bars mean ± standard error of the mean (SEM). *Different lowercase letters* indicate significant differences for the effect of land-use type (Tukey's test, $P < 0.05$) in each biotic group.

Woody plant diversity

A total of 41 woody species were recorded during sampling, of which 30 species were recorded in Mediterranean shrublands, 15 in dehesas, 22 in mixed-pine forests and five in olive groves (see Appendix C, Table 2).

At the sampling unit scale, the TD and FD of woody vegetation differed among land-use types ($F = 62.85$, $P < 0.0001$ and $F = 68.07$, $P < 0.0001$, respectively). Mediterranean shrublands had the highest TD values, followed by mixed-pine forests, with dehesas and olive groves having the lowest TD values (Fig. 2.2.1). By contrast, FD

was significantly higher in mixed-pine forests than in Mediterranean shrublands, with dehesas and olive groves having yet lower FD values (Fig. 2.2.1).

At the site scale, TD and FD also differed among studied land-use types, following similar patterns to those observed at the sampling unit scale ($F = 14.66$, $P < 0.0001$ and $F = 10.36$, $P = 0.0005$, respectively). However, the differences in TD between Mediterranean shrublands and mixed-pine forests, as well as those between mixed-pine forests and dehesas, were not significant. With respect to FD, while at the sampling unit scale there were differences between Mediterranean shrublands and dehesas, at the site scale this difference disappeared (Fig. 2.2.1).

Ant diversity

Six sampling units (three in Mediterranean shrublands, two in dehesas and one in mixed-pine forests) were eliminated because some pitfall traps were lost or damaged. Of the remaining 34 sampling units, a total of 33 species were captured, with 25 species recorded in Mediterranean shrublands, 23 in dehesas, 20 in mixed-pine forests and 22 in olive groves (see Appendix C, Table 3).

At the sampling unit scale, TD was significantly lower in mixed-pine forests and olive groves than in the other land-use types ($F = 15.28$; $P < 0.0001$; Fig. 2.2.1). Significantly higher FD was detected in Mediterranean shrublands than in mixed-pine forests and olive groves ($F = 8.62$; $P < 0.0001$; Fig. 2.2.1). By contrast, at the site scale, we found no difference in TD or FD among any of the land-use types ($F = 1.75$, $P = 0.175$ and $F = 0.533$, $P = 0.662$, respectively; Fig. 2.2.1).

Bird diversity

A total of 38 bird species were recorded during sampling, with 23 species recorded in Mediterranean shrublands, 26 in dehesas, 14 in mixed-pine forests and 23 in olive groves (see Appendix C, Table 4).

At the sampling unit scale, land use had a significant effect on bird TD ($F = 11.19$; $P < 0.0001$), which was significantly higher in dehesas than in the other land-use types (Fig. 2.2.1), with mixed-pine forests having the lowest values. However, FD exhibited no significant differences among land-use types ($F = 0.561$; $P = 0.641$). At the site scale,

TD showed a similar pattern, with higher diversity in *dehesas*, followed by Mediterranean shrublands, while mixed pine forests had the lowest values. In contrast, FD was significantly higher in mixed-pine forests than in the other land-use types (Fig. 2.2.1).

Partitioning of TD and FD at different levels of the sampling hierarchy

The overall partitioning of TD (Fig. 2.2.2) revealed that the TD of ants and birds was quite evenly distributed among the three observation levels of the sampling hierarchy, except for mixed-pine forests. In mixed-pine forests, most of the TD of ants was attributed to differences between sites (60.6 %), in contrast to that of birds (only 10.6 %). For herbaceous plants, most of the TD was observed between sites, ranging from 46.9 % in mixed-pine forests to 53 % in dehesas and Mediterranean shrublands and 62.3 % in olive groves. The partitioning of woody vegetation TD showed no consistent pattern among land-use types, with the three levels being evenly distributed in Mediterranean shrublands. Variability within sampling units of woody vegetation explained most of the diversity in mixed-pine forests, dehesas and olive groves.

The partitioning pattern of FD differed greatly from that of TD. For all four biotic groups, most of the variability in FD occurred within the sampling unit scale (with percentages of mostly >90 %), irregardless of land-use type (Fig. 2.2.2).

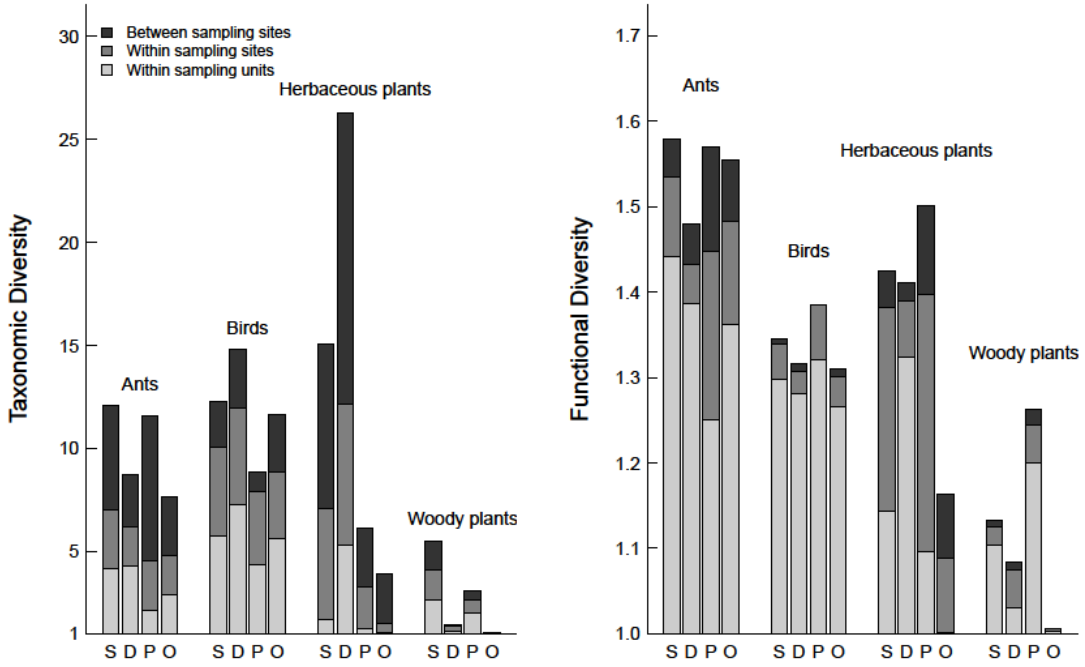

Fig. 2.2.2 Partitioning of the effective number of species (TD) and extent of index dissimilarity within communities (FD) at the different levels of the sampling hierarchy for each of the considered biotic groups and land-use types (*S* Mediterranean shrublands, *D* dehesas, *O* olive groves, *P* mixed-pine forests). *Within sampling units* diversity is the amount of diversity that is contained at the sampling unit scale, *within sampling sites* diversity is the amount of diversity that is attributed to differences among sampling units, *between sampling sites* diversity is the amount of diversity attributable to variability among sites. Given that the minimum number of equivalent species that can be partitioned is 1 and because these first species must be contained in the "Within sampling units" level, the minimum value of the *y-axis* is 1, which allows an easier comparison of the differences in the partitioning of FD between levels.

Relationship of FD and TD

The vectors of change for TD and FD along the studied gradient of land-use intensity (i.e. from Mediterranean shrublands to the other three land uses) showed clearly different patterns in the four biotic groups (Fig. 2.2.3). In the case of herbaceous and woody vegetation, vectors of change towards olive groves showed a decline for both TD and FD. In contrast, for land-use change to mixed-pine forests, we found no significant differences except for FD of woody vegetation. Regarding the transformation to

dehesas, the results showed an increase in TD for herbaceous plants and a decrease for woody plants, with FD remaining quite similar in both biotic groups (Fig. 2.2.3).

In the case of ants, changes along the land use gradient were less noticeable and non-significant (Fig. 2.2.3). A clear contrasting pattern was visible for birds. Land use change to mixed-pine forests showed that FD increased, whereas TD decreased, similar to the pattern observed for woody vegetation (Fig. 2.2.3).

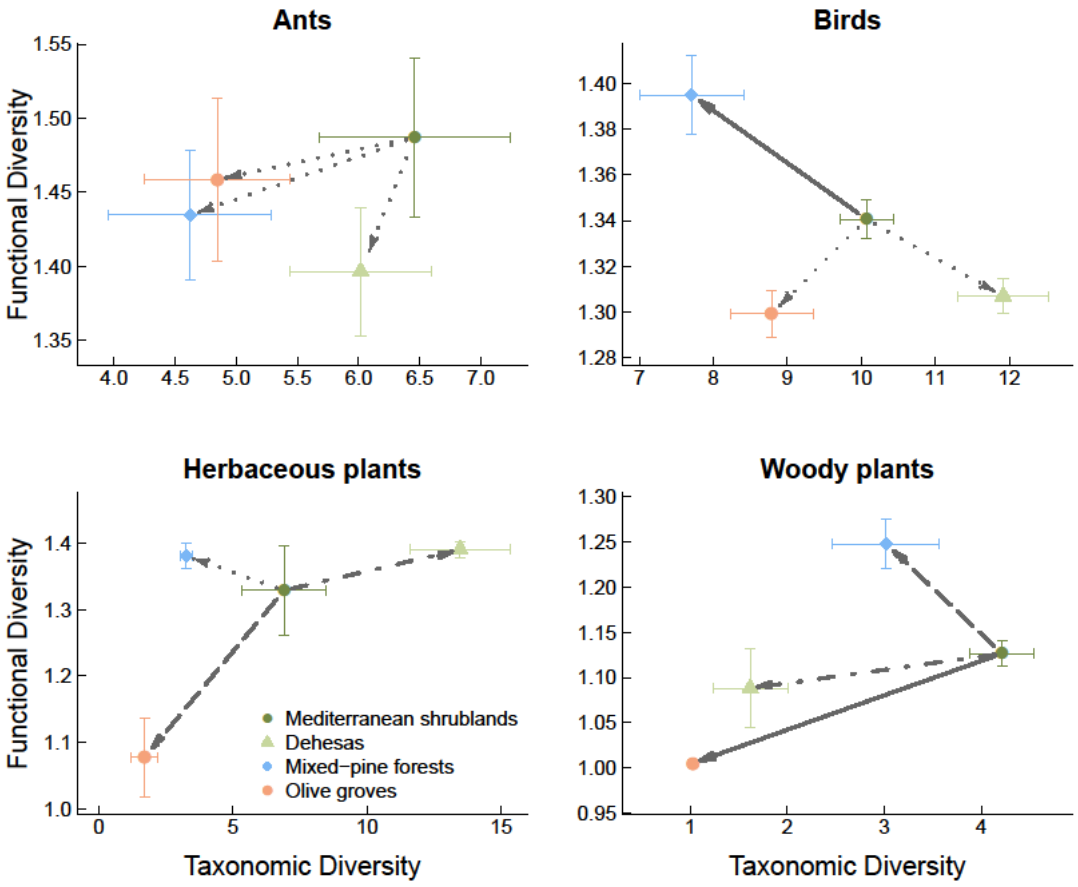

Fig. 2.2.3 The relationships of FD to TD in different land-use types for herbaceous plants (a), woody plants (b), ants (c) and birds (d) at the sampling site scale. *Arrows* indicate the vectors for changes in TD and FD from Mediterranean shrublands (considered as the natural vegetation in the study area) to the other land-use types. *Solid lines* Significant changes in both TD and FD, *dash-dot lines* significant changes in TD, *dashed line* significant changes in FD. Values are given as the mean ± SEM.

2.2.4 Discussion

Our results show that land-use transformation exerts important effects on biodiversity. However, in our study, these effects differed significantly among the various biotic groups and spatial scales studied. Moreover, we found that the two components of diversity analysed here (TD and FD) did not consistently vary with land-use change.

How do different biotic groups respond to changes in land‑use intensity?

Several studies have documented declines in the diversity of birds, mammals, plants and insects due to agricultural intensification at several spatial scales (Benton et al. 2002; Flynn et al. 2009; Breitbach et al. 2010). However, most of these studies have addressed their research questions by exploring a single taxonomic group or a single aspect of diversity. The few studies that have explored taxonomic and functional aspects of diversity simultaneously for several organism groups suggest that land-use effects on diversity are group-dependent (Flynn et al. 2009).

We found that herbaceous vegetation diversity declined after changes towards more intense land-use types, with the exception of *dehesas*, which showed the highest herbaceous TD (at both spatial scales analysed) and FD (at the sampling unit scale) values. These results may be due to (1) the elimination of competition with woody vegetation, resulting in more available resources for herbaceous vegetation, or (2) the effects of increased grazing, which reduces the abundance of dominant species, facilitating the presence of subordinate ones. Furthermore, livestock in *dehesas* plays a relevant role in seed dispersion, with potential positive effects on species diversity (Malo and Suárez 1995).

By contrast, our results on woody vegetation show a more complex pattern of response to land use. At both spatial scales, Mediterranean shrublands and mixed-pine forests had the highest TD values for woody vegetation, whereas mixed-pine forests had the highest FD values. This result may be due to the particular vegetation composition of mixed-pine forests in our study area, which present a singular mixture of native and introduced species. Consequently, the contrasting trait values of the pines (e.g. higher canopy height) with those of other woody species composing the understory resulted in a greater proportion of the functional space being occupied and, therefore, high FD

values. Indeed, further intensification leading to the disappearance of all woody species other than pines would probably cause a drastic reduction in FD.

We expected that ants, as semi-sessile organisms (Vandermeer and Yitbarek 2012), would exhibit a marked response to land use, similar to that recorded for herbaceous and woody vegetation. However, we did not detect any difference in TD or FD among land uses at the large scale. By contrast, at the sampling unit scale we detected reduced TD and FD (compared with Mediterranean shrublands) on mixed-pine forests and olive groves. This result may be due to the small-scale homogenisation effect caused by human practices, such as tillage or fumigation in olive groves, or to the continuous needle cover and shadow effect from pine plantations.

We found that birds exhibited lower TD with more intense land use, supporting previous research (Verhulst et al. 2004; Flynn et al. 2009). However, FD values did not follow a clear response pattern to land use at either of the spatial scales studied, in contrast with previous findings in Europe (Gregory et al. 2005). Notably, mixed-pine forests had the highest FD values and the lowest TD values for birds. These results indicate that the bird species present in mixed-pine forests are more functionally different from each other (i.e. fewer redundant species because changes in TD had little effect on FD; Petchey et al. 2007) compared to bird species identified in other land-use types. This pattern is similar to that observed for woody vegetation; thus, these two results may be correlated, whereby more functionally different tree growth forms are associated with more functionally distinct bird communities.

Finally, although not a goal of our study itself, future research that explores how functional traits between biotic groups are related through trophic interactions would be of high interest to complete our understanding of the effects of land-use intensification. This trait-based multitrophic perspective has been proposed as the next step forward for advancing biodiversity–ecosystem functioning research (Lavorel et al. 2013).

How does the spatial scale of analysis affect biodiversity changes?

Land-use change might exert changes in biodiversity at multiple spatial scales (Kleijn et al. 2009). We used two complementary analyses to assess the effects of spatial scale and land-use type on biodiversity. These two analyses provided different results. For example, no clear generalized pattern was observed when analysing the overall FD and

TD values at the two spatial scales being considered (diversity within sampling units and diversity within sites). In the case of ants, differences were found at the smaller scale, while no significant differences were detected at the larger scale. Ant diversity (both TD and FD) may vary across a wide range of spatial scales (Andersen 1997). The opposite occurred with the FD of birds, which showed no differences at the smaller scale but was significantly different at the larger scale, although only in mixed-pine forests. Regarding plants, both groups showed differences in TD and FD at both spatial scales. These results may be due to issues with the spatial scales used in our study, which may not have been sufficiently different. The potential differences in TD and FD might be more evident if compared at the regional (landscape) or global scale (Gotelli and Ellison 2002).

Alternatively, the analysis based on the additive partitioning of diversity (exploring α- and β-diversities) allowed us to better clarify the response of TD and FD to land-use transformation at different spatial scales. Previous studies have demonstrated that the additive partitioning of species diversity is particularly relevant and useful for analyzing the determinants of species diversity at multiple spatial scales and for designing more effective strategies for biodiversity monitoring and conservation (Veech et al. 2002; Carmona et al. 2012). In our case, we found clear contrasting patterns between TD and FD in the proportion of variability observed at each spatial scale. While most of the variability in TD was found at the larger scales ("within sampling sites" and "between sampling sites"), irregardless of organism group and land-use type, the greatest part of FD was found at the smallest scale of study ("within sampling unit"). This result indicates that species turnover among communities is much greater than functional trait turnover, which in turn shows that, for the traits selected for this research, the studied communities are ecologically redundant (de Bello et al. 2009). Although similar patterns have been previously described for plant communities (de Bello et al. 2009; Carmona et al. 2012), this is, to the best of our knowledge, the first time that it has been reported simultaneously for different taxonomic groups.

Do FD and TD follow similar patterns of change?

Human-induced land-use change usually causes species losses, and it is frequently assumed that this results in a loss of functional trait diversity. This is the most likely

response because FD (calculated using the Rao index or other indices) and TD are not completely independent of each other, but rather display a positive correlation (Laliberté and Legendre 2010). Mayfield et al. (2010) used the term "sampling effect" to refer to this positive relationship between species richness and FD observed in communities (Tilman et al. 1997). Accordingly, new traits will accumulate with the random addition of new species to a community or, similarly, traits will be lost when species are lost in a random fashion.

However, the responses of TD and FD could follow different patterns if the addition or loss of species is not random with respect to their functional traits. Particularly, if many species exhibit similar traits (i.e., they are redundant), the strength of the TD–FD relationship would be reduced (Naeem and Wright 2003). A concomitant loss of species and functional trait diversity would be, in these cases, just one of a range of potential responses to land-use change. Mayfield et al. (2010) proposed eight theoretical response trajectories (vectors of change) that might appear in natural communities affected by human-induced land-use change, with their occurrence being mostly determined by changes in processes of competitive exclusion and/or environmental filtering.

Our results are consistent with Mayfield's proposal, showing that the vectors of change in FD and TD exhibit very different response trajectories along a land-use intensity gradient and that the pattern of response is highly dependent on the biotic group under analysis. In the most extreme example of land-use transformation considered in our study (i.e., from Mediterranean shrublands to olive groves), the observed vectors of change in all biotic groups revealed a concurrent decrease in both TD and FD (although only significant for herbaceous and woody plants). However, our results are more heterogeneous when analysing land-use transformation to *dehesas* or mixed-pine forests.

Transformation to *dehesas* produced completely different results in all four studied biotic groups. Ant and bird diversity did not show significant patterns of change. In the case of herbaceous vegetation, there was a significant increase in species diversity, which was not matched by a similar change in functional trait diversity, resulting in an herbaceous community with high functional redundancy (i.e. the number of species possessing similar traits). This type of land-use transformation implies that the clearing of dense tree coverage relaxes competitive interactions and/or increases the availability of resources for herbaceous plants, allowing more functionally similar species from the

regional pool to coexist. *Dehesas*, as pastoral systems that were originally forested, might still support high levels of TD, associated with the replacement of a larger variety of growth forms for numerous species with the same herbaceous growth form. In *dehesas*, the functional redundancy of herbaceous vegetation illustrates how functional trait diversity and TD may be decoupled.

In the case of woody vegetation, the opposite was observed in the trajectory of change from Mediterranean shrublands to *dehesas*, with the noticeable decrease in TD not being matched by a decrease in functional trait diversity. In this case, woody species richness might have declined due to the increased importance of environmental filters, such as livestock grazing pressure on sprouting plants. If these species losses are evenly distributed across functional trait groups, then no corresponding loss of functional trait diversity would be expected.

In conclusion, our results support the argument that the relationship of land use with TD and FD is highly complex and context-dependent (Naeem and Wright 2003). Importantly, we demonstrate that changes in land use do not necessarily lead to the loss of FD mediated by the loss of species and/or functional traits, this effect being dependent on the biotic group analysed and the type and intensity of land transformation. Thus, conservation studies on the effects of land-use change should consider the particularities of each study site, the effect of spatial scale and biotic group when analysing the possible trajectories of change in both TD and FD.

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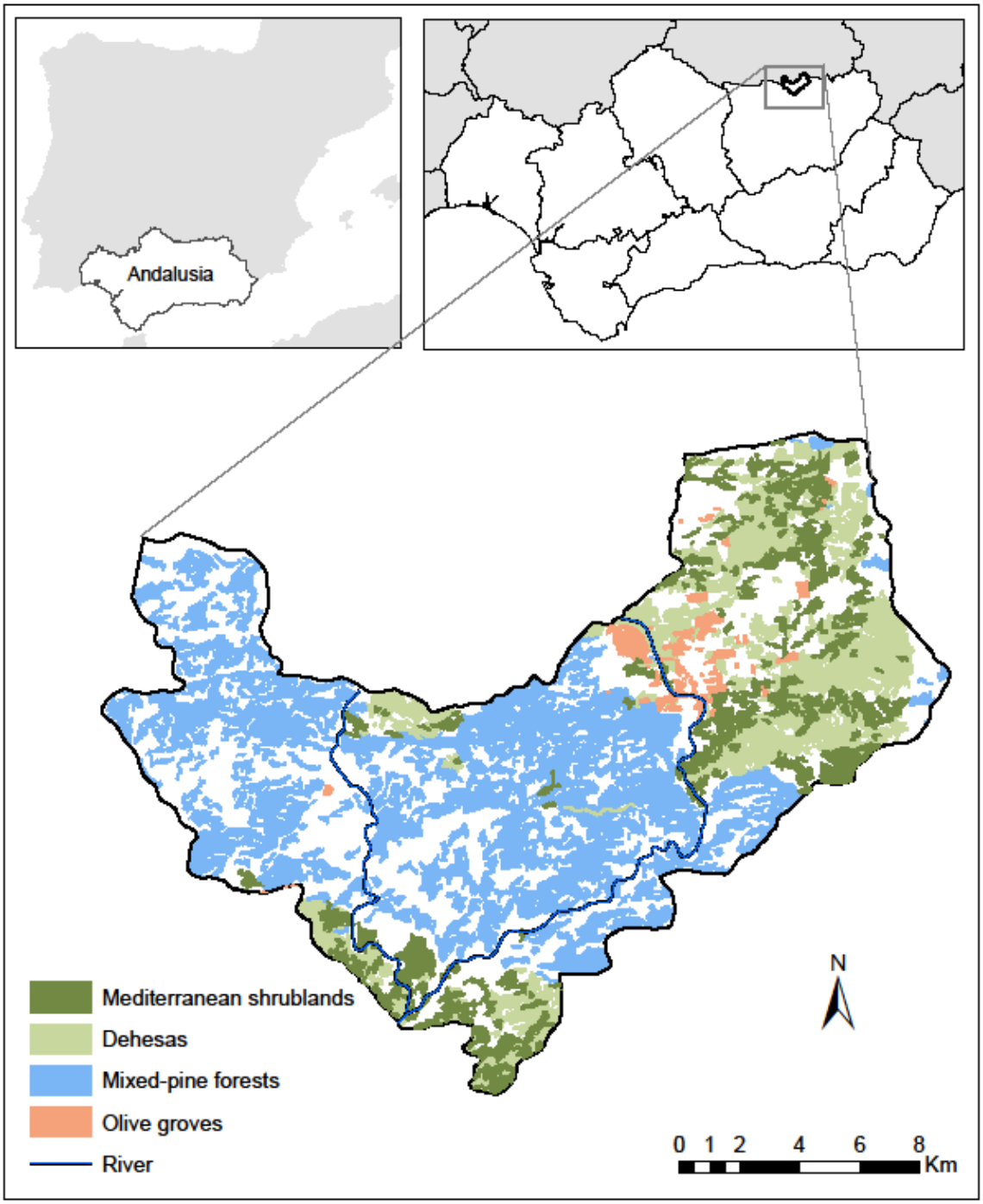
Apendix A. Map of the study area showing the surface occupied by the four dominant land use types (Mediterranean shrublands, dehesas, mixed-pine forests and olive groves).



Apendix B. Dominant land use types in the study area.

Mediterranean shrublands


Dehesas


Mixed-pine forests


Olive groves


Apendix C.

Table 1. Herbaceous species found on the different land use types sampled.

Species	Land use types			
	Mixed-pine forests	Olive groves	*Dehesas*	Mediterranean shrublands
Aegilops geniculata			X	
Agrostis castellana			X	
Agrostis pourretii			X	
Alyssum granatense			X	X
Andryala integrifolia			X	X
Anthemis arvensis		X	X	
Anthoxanthum aristatum			X	X
Anthyllis cornicina			X	
Anthyllis lotoides			X	
Aphanes microcarpa			X	X
Arrhenatherum album	X		X	X
Asterolinon linumstelatum	X		X	X
Avena barbata			X	X
Biserrula pelecinus			X	X
Brassica barrelieri		X	X	X
Briza minor				X
Bromus hordeaceus			X	X
Bromus rubens			X	X
Bromus sterilis	X			X
Calendula arvensis			X	X
Campanula hispanica			X	X
Carlina corymbosa	X			
Centaurea collina			X	
Cerastium semidecandrum		X		X
Coronilla minima	X		X	
Corynephorus fasciculatus			X	
Crepis capilaris			X	X
Crepis vesicaria			X	X
Crucianella angustifolia			X	X
Crucianella patula			X	X
Cynodon dactylon	X			
Dactylis glomerata	X			X
Daucus carota				X
Echium plantagineum			X	X
Erodium cicutarium			X	X
Eryngium campestre			X	X
Eryngium tenue			X	X
Euphorbia exigua			X	X
Evax carpetana			X	
Filago hitescens			X	
Fylago lutescens			X	X
Galium parisiense		X	X	X
Geranium molle			X	X
Hedypnois cretica			X	
Helianthemum aegyptiacum			X	

Species	Land use types			
	Mixed-pine forests	Olive groves	*Dehesas*	Mediterranean shrublands
Herniaria glabra			X	
Herniaria hirsuta			X	
Holcus setiglumis			X	
Hypochaeris glabra			X	X
Hypochaeris radicata			X	X
Lactuca tenerrina				X
Leontodon taraxacoides			X	X
Logfia gallica	X		X	
Logfia minima			X	
Lolium rigidum			X	X
Medicago polymorpha			X	
Micropyrum tenellum			X	X
Ornithopus compressus			X	
Paronychia argentea			X	
Plantago coronopus			X	
Plantago lagopus			X	
Poa annua			X	
Poa bulbosa			X	
Psilurus incurvus			X	
Rumex angiocarpus	X		X	X
Rumex bucefalophorus			X	
Sanguisorba minor			X	X
Scleranthus annus			X	
Scolymus hispanicus			X	X
Silene gallica			X	
Spergula arvensis			X	
Spergularia purpurea			X	X
Taeniatherum caput-meduseae			X	
Thapsia villosa			X	
Tolpis barbata			X	X
Trifolium angustifolium			X	
Trifolium arvense			X	
Trifolium campestre			X	X
Trifolium cherleri			X	X
Trifolium dubium			X	X
Trifolium glomeratum			X	X
Trifolium hirtum			X	
Trifolium micranthum			X	X
Trifolium stellatum			X	
Trifolium striatum			X	
Veronica arvensis				X
Viola kitabeliana			X	X
Vulpia ciliata			X	X
Vulpia membranacea			X	
Vulpia muralis			X	X
Vulpia myuros		X	X	X
Xolantha guttata			X	

Table 2. Woody species found on the different land use types sampled.

Species	***Land use types***			
	Mixed-pine forests	Olive groves	*Dehesas*	Mediterranean shrublands
Arbutus unedo			X	X
Asparagus acutifolius		X	X	X
Asphodellus albus	X		X	X
Bryonia dioica		X	X	
Carduus tenuiflorus				
Cistus albidus				X
Cistus clusii			X	X
Cistus ladanifer	X		X	X
Cistus monspeliensis				X
Cistus populifolius	X		X	
Cistus salvifolius			X	X
Clematis vitalba				
Crataegus monogyna				X
Cytisus scoparius	X		X	X
Daphne gnidium	X		X	X
Erica arborea	X		X	X
Erica australis	X			
Fraxinus angustifolia				X
Genista florida	X			
Glycyrrhiza glabra	X			
Halimium umbellatum				X
Helichrysum stoechas				X
Juniperus oxycedrus	X			X
Lavandula stoechas	X			X
Olea europaea		X		X
Paeonia	X		X	X
Phillyrea angustifolia	X			X
Phlomis purpurea				X
Pinus pinaster	X			
Pinus pinea	X			
Pistacia lentiscus	X	X		X
Pistacia terebintus				
Pyrus spinosa				X
Quercus ballota	X	X	X	X
Quercus coccifera	X			X
Quercus faginea	X		X	X
Quercus suber	X			X
Rosmarinus officinalis	X			X
Ruta graveolens				
Thymus mastichina	X			X
Ulex parviflorus			X	X

Table 3. Ant species found on the different land use types sampled.

Species	***Land use type***			
	Mixed-pine forests	Olive groves	*Dehesas*	Mediterranean shrublands
Aphaenogaster dulcineae		X		X
Aphaenogaster gibbosa	X	X	X	X
Solenopsis monticola	X	X	X	
Stenamma debile	X			
Temnothorax recedens	X			
Temnothorax tristis cfr	X	X		
Temnothorax pardoi	X			X
Camponotus fallax				
Camponotus lateralis	X			
Camponotus truncatus				
Lasius lasioides		X		X
Lasius niger cfr		X		
Aphaenogaster iberica	X	X	X	X
Crematogaster auberti	X	X	X	X
Crematogaster scutellaris	X		X	
Crematogaster sordidula				X
Formica fusca	X			X
Pheidole pallidula	X	X	X	X
Plagiolepis schimitzii	X	X	X	X
Tapinoma nigerrimum		X	X	X
Tetramorium semilaeve	X	X	X	X
Camponotus cruentatus	X	X	X	X
Camponotus foreli		X	X	X
Camponotus micans			X	
Camponotus piceus				X
Camponotus pilicornis	X			X
Cataglyphis iberica	X	X	X	X
Cataglyphis rosenhauri		X	X	X
Formica gerardi	X			X
Formica subrufa	X	X		X
Gonomma hispanicum			X	X
Messor barbarus		X	X	
Messor bouvieri		X	X	X
Oxyopomyrmex saulcyi			X	X
Proformica ferreri	X			

Table 4. Bird species found on the different land use types sampled.

Species	***Land use types***			
	Mixed-pine forests	Olive groves	*Dehesas*	Mediterranean shrublands
Aegithalos caudatus		X	X	X
Alauda arvensis		X	X	
Alectoris rufa		X	X	
Athene noctua		X	X	
Carduelis carduelis	X	X	X	X
Carduelis chloris	X	X		X
Certhia brachydactyla	X			X
Cisticola juncidis				X
Columba palumbus	X	X	X	X
Cyanopica cyana		X	X	X
Dendrocopos major	X			
Erithacus rubecula		X		
Fringilla coelebs	X	X	X	X
Galerida cristata		X	X	
Garrulus glandarius	X	X	X	X
Lanius senator			X	
Lullula arborea		X	X	X
Merops apiaster			X	X
Muscicapa striata	X			X
Oriolus oriolus			X	X
Otus scops		X		X
Parus caeruleus	X	X	X	X
Parus cristatus	X			X
Parus major	X	X	X	X
Passer domesticus		X	X	
Pica pica		X	X	X
Picus viridis			X	X
Regulus ignicapillus	X			
Sitta europaea	X			
Streptopelia decaocto		X		X
Streptopelia turtur		X	X	X
Sturnus unicolor		X	X	X
Sylvia cantillans			X	X
Sylvia undata			X	
Turdus merula	X	X	X	X
Turdus philomelos			X	
Turdus viscivorus			X	X
Upupa epops		X	X	

Capítulo 2.3

Explorando el papel de las vías pecuarias trashumantes en la conservación de la diversidad de hormigas en agroecosistemas mediterráneos

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2.3 Exploring the role of transhumance drove roads on the conservation of ant diversity in Mediterranean agroecosystems

Abstract

Drove roads are a major feature of Mediterranean countries, where this livestock management system has been practiced for centuries. In Spain, many drove roads have become completely or partially abandoned by herders, and transformed for other land uses. Yet, some major drove roads continue to be used for the passage of livestock, and might exert important effects on the conservation of biodiversity and ecosystem functions, particularly in highly transformed agricultural landscapes. In this study, we compare ant taxonomic and functional diversity on a drove road that is still used by transhumant livestock (the Conquense Drove Road) versus an abandoned road (the Murciana Drove Road). Ant species richness per trap and ant richness per sample unit were significantly higher on the used drove road compared to the abandoned drove road. The used drove road also had a positive edge effect on ant species diversity in adjacent croplands (both herbaceous crops and vineyards). Ant functional diversity was also higher on the used drove road. These results draw attention to the role of drove roads as ecologically unique systems and reservoirs of biodiversity, particularly within intensive agricultural landscapes. These effects, however, are largely dependent on maintaining livestock use.

Keywords: Ants, Biodiversity, Functional diversity, Transhumant pastoralism

2.3.1 Introduction

Traditional management practices have been widely recognized for their role in the conservation of biodiversity in agricultural landscapes, both in academia and in the political arena (Fischer et al. 2012; Oppermann et al. 2012; Wright et al. 2012). Distinctive characteristics of traditionally managed agroecosystems that are associated with higher levels of biodiversity include: substantial amounts of natural or seminatural vegetation and high heterogeneity in land cover at a fine spatial grain (Plieninger et al. 2006), low-input technology under local ecological knowledge systems, and taking full advantage of natural ecological processes (Altieri et al. 1987; Perrings et al. 2006). The emerging concept of ‘‘High Nature Value farming’’ in Europe has developed from the growing recognition that the conservation of biodiversity is highly dependent on the continuation of traditionally managed, low-intensity farming systems (Oppermann et al. 2012). This is particularly true in the Mediterranean Basin, which is a widely recognized biodiversity hotspot (Myers et al. 2000), where traditional management practices are responsible for shaping biologically rich ‘‘cultural’’ landscapes as a result of many centuries of dynamic interaction between people and their natural environment (Blondel 2006).

Transhumance represents one such traditional management practice that was developed by ancient Mediterranean societies to cope with a highly seasonal climate, allowing shepherds to balance the herd’s need for forage material with seasonal peaks in pasture availability (Manzano-Baena and Casas 2010). Transhumance involves the seasonal movement of livestock between upland areas (or higher latitudes) and lowland areas (or lower latitudes), where the livestock occupy summer or winter pastures, respectively (Ruiz and Ruiz 1986; Oteros-Rozas et al. 2012a).

Transhumant livestock movements are a widespread phenomenon worldwide (Olea and Mateo-Tomás 2009), and usually follow traditional routes called drove roads (or drover roads or droveways). Drove roads exist in many countries; however, Spain constitutes a unique case, as the traditional network of drove roads has been in use for centuries and was granted legal protection in 1995 (Drove Roads Act). The network is formed by a mixture of Royal Drove Roads (*Cañadas Reales*), with a legal width of ca. 75 m, and smaller trails, known as *cordeles* (ca. 37 m wide) and *veredas* (ca. 20 m). The entire

network covers nearly 1 % of the country, spreading across more than 125,000 km, and covering 421,000 ha in total (Merino and Alier 2004).

Transhumant pastoralism in Spain is currently in decline, being generally perceived as a relict activity (Oteros-Rozas et al. 2012b). Nevertheless, the Spanish government, environmental organizations, and academics have widely recognized the historical, cultural, scenic, and ecological value of transhumance (e.g., Bunce et al. 2004; MARM 2011). For instance, drove roads have been reported to serve as ecological corridors, facilitating connectivity among plant and animal populations (Gómez-Sal and Lorente 2004); thus, drove roads contribute towards maintaining genetic diversity, which would otherwise be diminished by general habitat fragmentation (Fahrig 2003). Livestock that moves along drove roads also serve as a vector for the seed dispersal of many plant species, enriching the biodiversity of connected territories (Manzano and Malo 2006).

Most landscapes that are crossed by major drove roads in Spain are characterized by intensive agricultural practices. Agricultural intensification has been considered as one of the major causes of biodiversity decline (Tilman et al. 2002). Although the magnitude of the effect of intensification might be dependent on farmland features and management options, there is no doubt that, as agriculture becomes more intensive, biodiversity decreases (Krebs et al. 1999). As a result, agri-environment schemes have been promoted by the Common Agricultural Policy (CAP) of the European Union. These schemes aim to alleviate the ecological impact of modern, intensive agriculture, through rewarding farmers who foster biodiversity by adopting environmentally friendly ways of managing the land (i.e., by enhancing landscape multifunctionality). However, to improve the effectiveness of agri-environment schemes and develop effective monitoring systems, it is crucial to identify management practices and landscape configurations that are more beneficial to biodiversity. In this context, drove roads deserve attention. In the case of Spain, drove roads consist of linear strips of natural grassland vegetation crossing a highly transformed agricultural matrix; hence, drove roads might enhance resilience by creating a mosaic of patches with varied functions, habitat heterogeneity, and landscape diversity (Coughenour 2007). In parallel, drove roads act as a source of important ecosystem services (Oteros-Rozas et al. 2012a), and as reservoirs of biodiversity (Bunce et al. 2004; Azcárate et al. 2012).

Ants have been proposed as a good indicator group of changes in ecosystems, since they are widespread, moderately diverse, functionally significant, and easy to sample

(Alonso and Agosti 2000). Furthermore, ants are relatively sedentary, and hence sensitive to changes in the environment that arise at small scales in space and time (Bestelmeyer and Wiens 1996). Ants play an important role in ecological flows, and participate in a wide range of ecological interactions (Ho¨lldobler and Wilson 1990; Alonso and Agosti 2000; Franklin 2012). In addition, ant responses to environmental stress and disturbance are relatively well-understood compared to other invertebrates (Hoffmann and Andersen 2003). Moreover, they are sensitive to changes in soil condition within agricultural systems (Peck et al. 1998). Thus, ants may be a useful tool when monitoring changes in fauna related to agricultural practices (Andersen and Majer 2004). Furthermore, ants are an important part of the animal biomass, and act as engineer species (Folgarait 1998). For instance, recent data show that the presence of ants contributes positively to improve certain physico-chemical properties of soils (including the presence of mineral nitrogen, increased porosity, and water infiltration) in areas with a dry climate and intensive agriculture (Evans et al. 2011).

The relationship between species diversity and ecosystem function is known to be complex and context dependent (Naeem and Wright 2003). Traditionally, species richness has been used as the best way to quantify species diversity (Duelli and Obrist 1998; Krewenka et al. 2011). However, in recent years, many studies have focused on assessing functional diversity (Flynn et al. 2009; Laliberté et al. 2010) because it may be directly linked to ecosystem processes (Reiss et al. 2009).

In this contribution, we explore how the presence of a drove road within an intensive agricultural landscape influences the taxonomic and functional diversity of ants. Specifically, we compare two drove roads surrounded by similar agroecosystems, one still in use by transhumant livestock and one that has been abandoned. Within this framework, we analyze differences in ant species composition, species richness, and functional diversity between the two drove roads and between the drove roads and their adjacent croplands. Finally, we discuss the implications of maintaining livestock use of drove roads for the conservation of biodiversity and ecosystem functions in intensive agricultural landscapes.

2.3.2 Methods

Study area

The study site is a fairly homogeneous area in the Autonomous Community of Castilla-La Mancha (Spain), within the municipalities of Las Pedroñeras, Casa de los Pinos, and Villarrobledo (Fig. 2.3.1). The area is an open plain, at an altitude of about 800 m a.s.l., and is characterized by a continental Mediterranean climate (mean annual precipitation: 461 mm; mean annual temperature: 14 ºC). The lithology is mainly composed of gravels, conglomerates, sands, and sandstone. The predominant land use types are intensive agricultural systems of cereals, onion, garlic, and vineyards.

Two major drove roads, officially demarcated with boundary stones, cross the agricultural landscape of the study area: the Conquense Drove Road (CDR) and the Murciana Drove Road (MDR) (Fig. 3.3.1). The CDR is one of the few major drove roads in Spain that still maintains livestock use on foot every year. Fifteen transhumant herders, with almost 8,900 sheep and 250 cows, cross this drove road twice a year in a 25–30-day trip between the summering areas located in the mountain pasturelands of Montes Universales and Serranía de Cuenca (Teruel, Cuenca and Guadalajara provinces) and the southern *dehesas* of Sierra Morena (Jaén and Ciudad Real provinces), approximately 410 km away (Oteros-Rozas et al. 2012a). In contrast, the MDR is an abandoned branch that connects with pasturelands in the Murcia province, and has not been used by transhumant livestock for more than 20 years (Bacaicoa et al. 1993). The vegetation of the two drove roads is mostly composed of Mediterranean grasslands dominated by therophyte species, although some parts of the MDR have been invaded by neighboring croplands, as a consequence of the lack of livestock use.

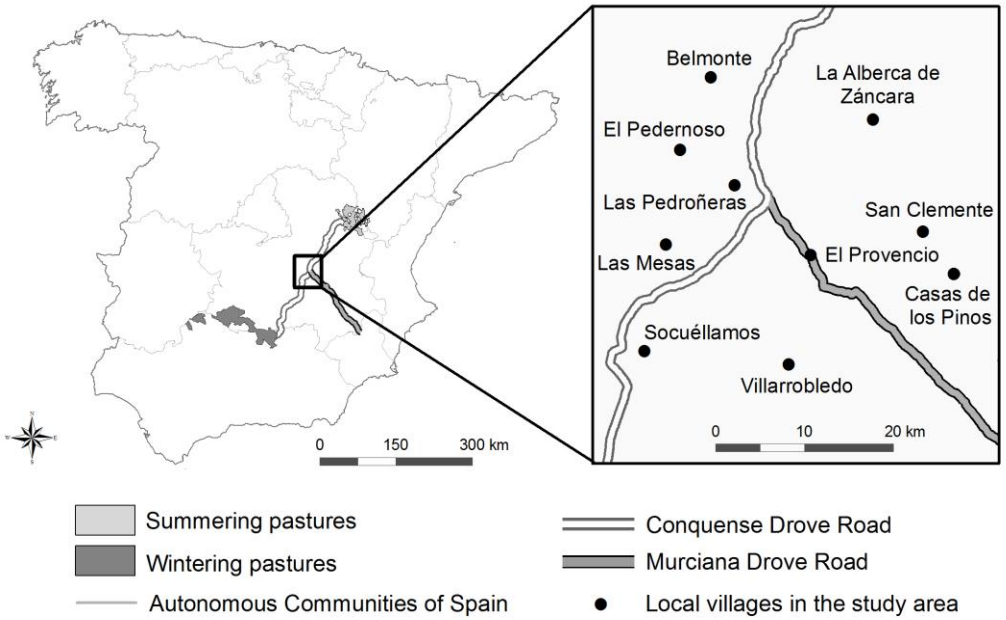

Fig. 2.3.1 Study area location, showing the Conquense Drove Road (with its summering and wintering pasturelands) and the Murciana Drove Road.

Sampling design and data collection

Two sections of these drove roads, sharing the same biogeophysical characteristics (Supplementary material 1) and situated 14 km apart, were selected for sampling. Sixteen sampling units were positioned on the CDR area and 16 on the MDR area. Since crop type may have an important effect on ant community composition (Perfecto et al. 2003; Rosumek et al. 2009), eight sampling units of each drove road were randomly located in environments with herbaceous crops, while the other eight sampling units were located in environments with vineyards. The distance between sampling units ranged from 291 to 730 m. For each sampling unit, we made one observation *within the drove road and one observation in the croplands adjacent to the drove road*. Each observation consisted of a group of six pitfall traps that were placed systematically every 10 m at a 30º angle (Fig. 2.3.2). Traps were 2 cm in diameter and 5 cm deep, containing a mixture of 70 % ethanol and 30 % monoethylene glycol (Azcárate and Peco 2011). The traps were placed on 27 July 2011 and collected on 3 August 2011. Despite some limitations, pitfall traps are considered the most objective and fast method to sample ants that live in soil (Andersen 1991; Nash et al. 2004), being recommended for intersite comparisons (Schmidt et al. 2012).

Ants were identified to the species-level with a binocular microscope, and were thencharacterized according to: (a) head length, (b) functional group, and (c) trophic-basedclassification. Head length was used as a proxy for overall body size (Kaspari and Weiser 1999), and was measured as the maximum longitudinal length from the most anterior part of the clypeus to the occipital margin, in full face view (Espadaler 2001). We considered functional groups from the perspective of Gitay and Noble (1997); namely, groups of species that respond to disturbance and stress in a similar way. We followed the classification by Roig and Espadaler (2010), who delineated eight functional groups: invasive and/or exotic (IE), generalists and/or opportunistic (GO), social parasites (P), specialist predators (SP), coarse woody debris specialists (CWDS), cold-climate specialists and/or shade habitats (CCS/SH), hot climate specialists and/or open habitats (HCS/OH), and cryptic (C). This classification was adapted from Brown (2000) for the Iberian Peninsula and Balearic Islands. Based on existing literature (Azcárate and Peco 2011) and our field experience at the study site, we assigned four non-exclusive trophic categories to the ant species; specifically, honeydew, live prey, seeds, and scavenger.

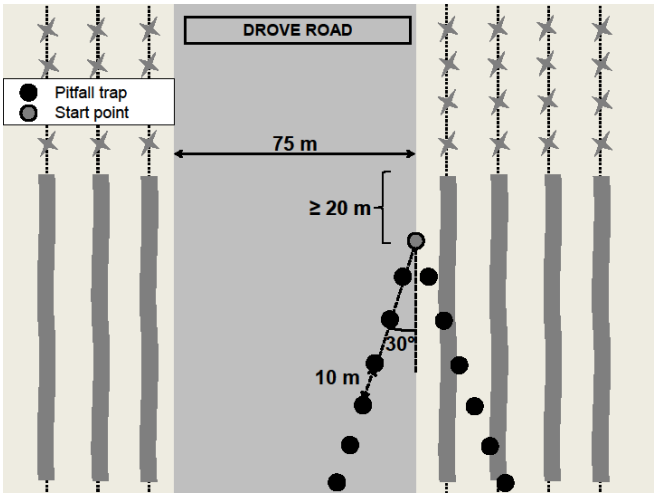

Fig. 2.3.2 Schematic representation of the sampling design. This method was carried out at each of the 32 sampling units that were placed in the area of the two drove roads.

Data analysis

Each observation was characterized by ant species composition, ant richness per sample unit, ant richness per trap, and ant functional diversity. The number of individuals

captured in traps was recorded, but not taken into account for the analyses, because it might have been highly influenced by the position of nests (Andersen 1991).

Ant species composition was defined as the number of occurrences (0–6) of each species at each observation. To simplify the composition of species to fewer dimensions, and facilitate interpretation, observations were organized by a non-metric multidimensional scaling based on Euclidean distances and a stress limit of 0.2. The position of observations in each of the two axes was analyzed by a MANOVA test, with two between subject factors (*livestock use* and *crop type*) and one within-subject factor (*drove road*).

To analyze the effect of livestock use and crop type on ant richness per sample unit and ant richness per trap, ANOVA tests were performed with two between-subject factors (*livestock use* and *crop type*) and one within-subject factor (*drove road*). Subsequently, we carried out a post hoc Tukey test to analyze differences between the different levels of the three factors.

Regarding functional diversity, we computed a new matrix of species functional dissimilarities using the Gower distance to calculate functional diversity, with the three traits (head length, functional group, and a trophic-based classification), each with equal weighting (i.e., one third) in the calculations. Ant functional diversity for each observation was calculated using the Rao index of diversity (1), which is widely accepted as an efficient functional diversity index. Because the Rao index of diversity is a generalization of the Simpson's index of diversity, it may be used with various measures of dissimilarity between species, and has an intuitive interpretation (Leps et al. 2006):

$$FD_{Rao} = \sum_{i=1}^{5} \sum_{j=1}^{5} d_{ij}\, p_i\, p_j$$

where d_i expresses the dissimilarity between each pair of coexisting species i and j. FDRao varies from 0 (when two species have the same traits) to 1 (when two species have completely different traits). In the event of binary or categorical traits, $d_{ij} = 0$ when the species have the same trait value, and $d_{ij} = 1$ when the species have different trait values. Since FD_{Rao} did not fulfill the normality and homoscedasticity requirements for parametric tests, we used a Wilcoxon test to analyze the effect of the drove road factor, and two Mann–Whitney U tests to analyze the effect of livestock use and crop type.

Data processing and statistical analyses were performed using the software STATISTICA 8.0.

2.3.3 Results

Ant species richness

Six sampling units (one in the vineyard CDR, three in the herbaceous crop CDR, one in the herbaceous crop MDR, and one in the vineyard MDR) were eliminated, because of some pitfall traps being lost or damaged. For the remaining 26 sampling units, a total of 6,513 ant workers belonging to 26 species were captured (Table 2.3.1). Twenty-five species were recorded at the CDR area (of which 12 were exclusive to this drove road), and 14 at the MDR area (of which 1 was exclusive to the adjacent vineyards).

Ant richness per sample unit was significantly higher on the CDR than on the MDR ($F_{1,28} = 48.486$, $P < 0.001$). Ant richness per sample unit was also significantly higher on the CDR than in the adjacent croplands ($F_{1,28} = 22.207$, $P < 0.001$). We did not detect significant differences for this variable among different crop types ($F_{1,28} = 0.045$, $P = 0.834$). In addition, ant richness per sample unit in herbaceous crops adjacent to the CDR was significantly higher than on the MDR (Tukey's test, $P < 0.01$). However, ant richness per sample unit in vineyard crops adjacent to the CDR was not significantly different to vineyard or herbaceous crops adjacent to the MDR (Tukey's test, $P > 0.05$; Fig. 2.3.3). Higher species richness at the CDR area was not only associated with generalist and/or opportunistic species (65 % higher), but particularly with hot climate and/or open habitat specialist species (125 % higher) (Fig. 2.3.4).

Table 2.3.1 Ant species found on drove roads (DR), along with the functional groups (FG) to which they belong (CCS/SH cold-climate specialists and/or shade habitats, C cryptic, GO generalists and/or opportunistic, HCS/OH hot climate specialists and/or open habitats).

Species	FG	CDR				MDR			
		Herbaceous		Vineyard		Herbaceous		Vineyard	
		DR	Crop	DR	Crop	DR	Crop	DR	Crop
Lasius grandis	CCS/SH	X	X	X	X	X	X	X	X
Temnothorax universitatis	C	X	X		X	X	X		
Solenopsis monticola	C				X				
Aphaenogaster gibbosa	C	X	X	X	X				X
Tapinoma madeirense	GO	X	X	X	X	X	X	X	X
Tapinoma nigerrimum	GO	X	X	X	X	X	X		X
Pheidole pallidula	GO	X	X	X	X	X	X	X	X
Crematogaster auberti	GO	X		X					
Crematogaster sordidula	GO			X					
Cardiocondyla batesii	GO	X		X					
Aphaenogaster iberica	GO	X	X	X	X			X	X
Aphaenogaster senilis	GO	X	X					X	
Tetramorium caespitum	GO		X						X
Tetramorium forte	GO	X	X			X	X		X
Tetramorium semilaeve	GO	X	X						
Cataglyphis rosenhaueri	HCS/OH	X	X	X	X	X	X	X	X
Messor barbarus	HCS/OH	X	X	X	X	X	X	X	X
Messor structor	HCS/OH	X	X						
Cataglyphis iberica	HCS/OH	X	X	X	X	X	X	X	X
Messor bouvieri	HCS/OH	X	X	X					
Messor hispanicus	HCS/OH	X		X					
Oxyopomyrmex saulcyi	HCS/OH								X
Camponotus micans	HCS/OH	X		X					
Camponotus aethiops	HCS/OH	X	X	X	X				
Camponotus sylvaticus	HCS/OH	X							
Camponotus foreli	HCS/OH			X					

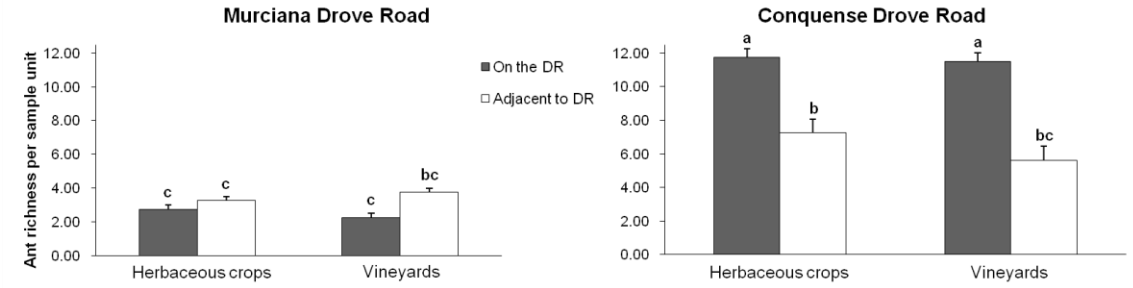

Fig. 2.3.3 Ant richness per sample unit on the two drove roads. *Error bars* represent mean ± standard error. *Different letters* indicate significant differences for this variable (Tukey's test, P\0.05) (DR drove road).

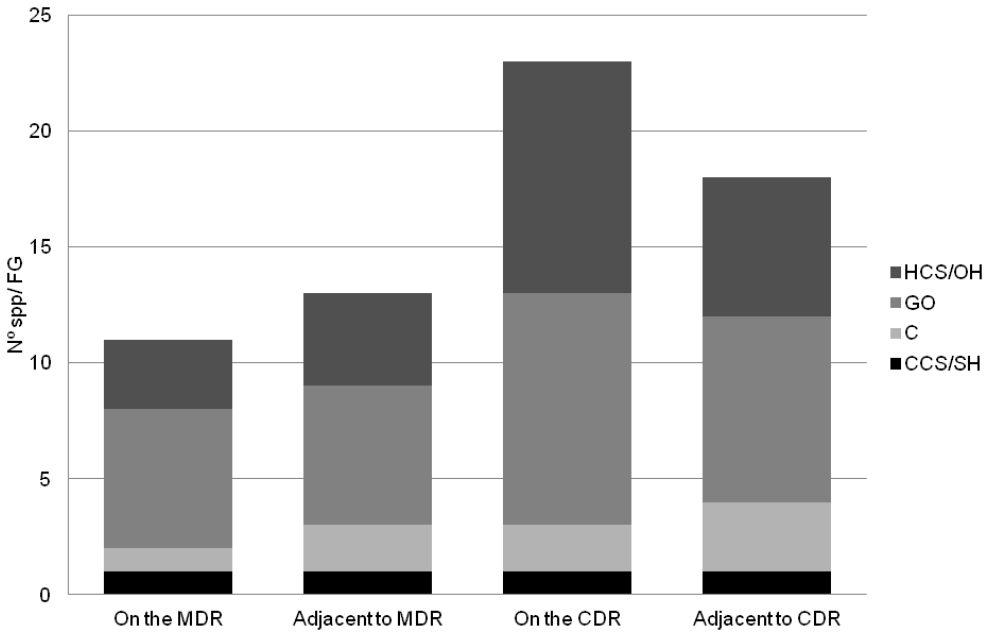

Fig. 2.3.4 Number of ant species for each functional group on the two drove roads (*CCS/SH* cold-climate specialists and/or shade habitats, *C* cryptic, *GO* generalist and/or opportunistic, *HCS/OH* hot climate specialist and/or open habitats, *CDR* Conquense Drove Road, *MDR* Murciana Drove Road).

Species richness per trap was higher on the CDR than on the MDR ($F_{1,28}$ = 27.42, P < 0.001). Richness per trap was also higher on the CDR than in adjacent croplands ($F_{1,28}$ = 25.02, P < 0.001). Crop type did not yield significant differences ($F_{1,28}$ = 0.87, P = 0.358), although herbaceous crops adjacent to the CDR showed a significantly higher value compared to the abandoned drove road and its adjacent areas (Tukey's test, P < 0.05; Fig. 2.3.5).

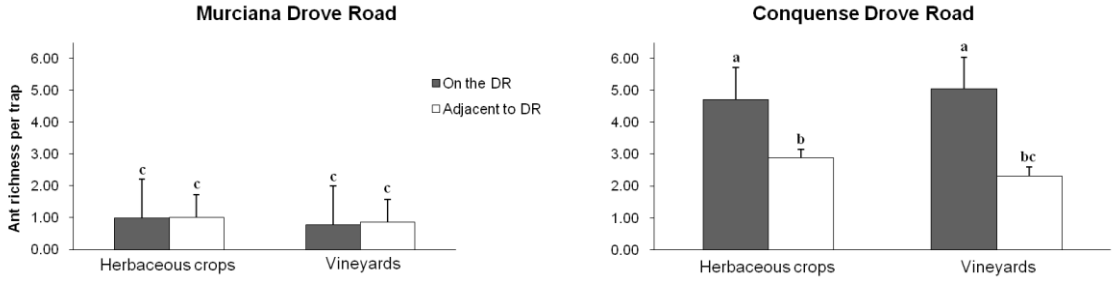

Fig. 2.3.5 Ant richness per trap on the two drove roads. *Error bars* represent mean ± standard error. *Different letters* indicate significant differences for this variable (Tukey's test, P < 0.05) (*DR* drove road).

Ant species composition

Non-metric multidimensional scaling of ant species composition revealed three main groups of observations: (1) the abandoned drove road and its adjacent fields, (2) the inside of the drove road in use, and (3) the croplands adjacent to the drove road in use (stress = 0.148) (Fig. 2.3.6). The positioning of the observations in the multidimensional scaling was dependent on livestock use ($F_{2,27}$ = 81.72; P < 0.001) and the drove road ($F_{2,27}$ = 44.89; P < 0.001). However, there were no significant differences in relation to crop type ($F_{2,27}$ = 0.4479; P > 0.05).

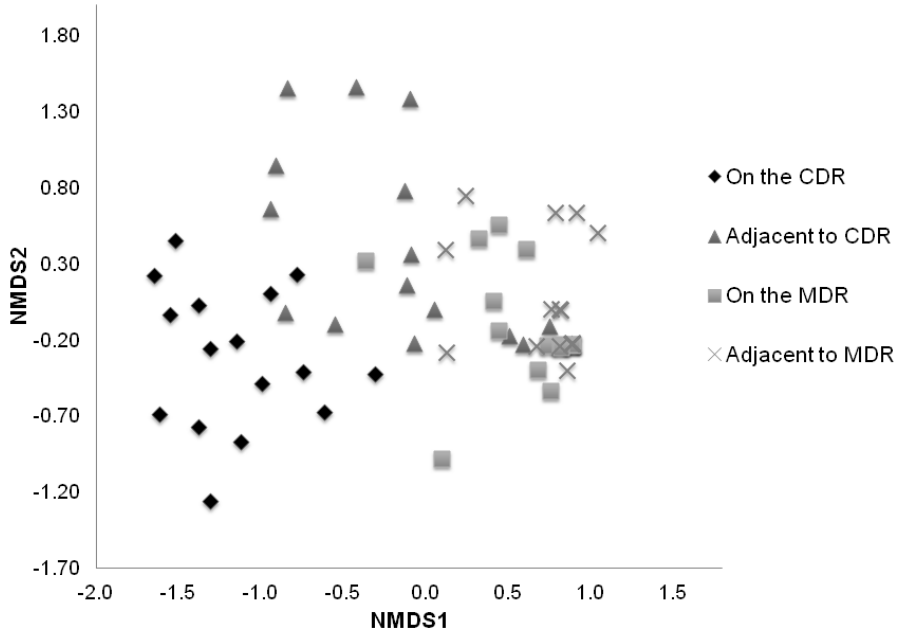

Fig. 2.3.6 Non-metric multidimensional scaling (NMDS) of ant species composition on the two drove roads. Dissimilarities were calculated by Euclidean distance (*CDR* Conquense Drove Road, *MDR* Murciana Drove Road).

Functional diversity

The Rao index showed significantly higher values on the CDR compared to the MDR (U = 10; P < 0.05). We also found significant differences between samples on the drove roads and samples in their adjacent croplands; higher values on the CDR compared to adjacent croplands (Z = -2.741; P < 0.05), but lower values on the MDR compared to

adjacent croplands (Z = -2.353; P < 0.05). Functional diversity did not respond to crop type in any of the compared areas (on the CDR: U = 31; P > 0.05; croplands adjacent to CDR: U = 18; P > 0.05; on the MDR: U = 29; P > 0.05; croplands adjacent to MDR: U = 30; P > 0.05) (Fig. 2.3.7).

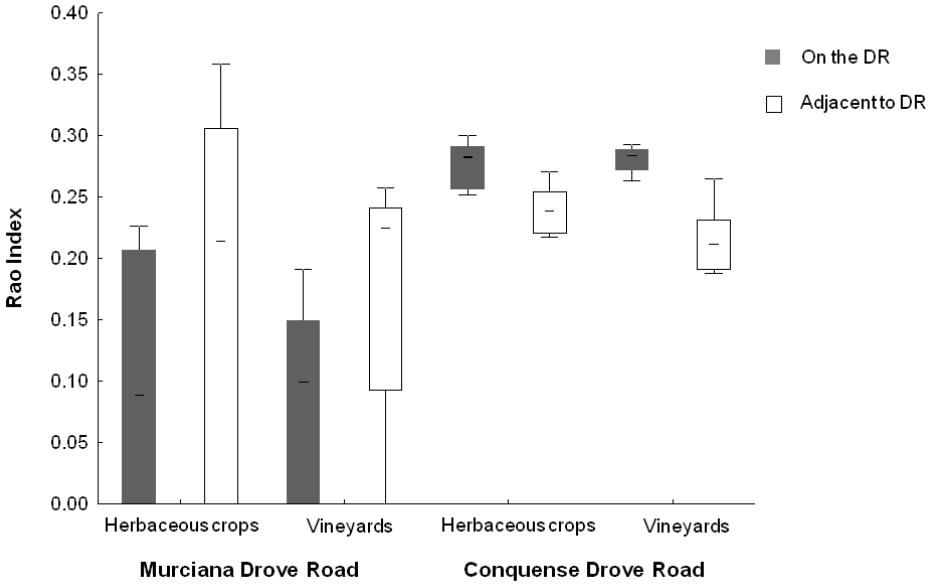

Fig. 2.3.7 Rao index values on the two drove roads. The *boxes* represent the three quartiles, and the whiskers represent the minimum and maximum values obtained for this variable (*DR* drove road).

2.3.4 Discussion

Ant diversity and drove roads

Our results suggest that the presence of a well-preserved drove road used by livestock might have significant effects on ant assemblages. Ant taxonomic diversity was significantly higher on the used drove road compared to the abandoned drove road. Moreover, the edges of croplands adjacent to the used drove road showed greater ant taxonomic diversity compared to the abandoned drove road and its adjacent croplands. In contrast, ant assemblages on the abandoned drove road were minimally different from those on the edges of adjacent croplands.

The simplest explanation for these differences is that the active drove road habitat is more favorable for ants. For instance, the environment of the used drove road has

minimal or no inputs of agrochemicals, but periodical inputs of manure. Yet, the absence of tilling within the drove road reduces disturbance compared to the adjacent cropland matrix. These factors might influence the quantity and variety of food that is available to ants, which might explain the observed differences in species composition and taxonomic diversity between the two roads. Some agricultural practices (e.g., soil fertilization by chemical inputs, plowing, and irrigation) have been related with a reduction in ant diversity and ant colony density (Díaz 1991). These practices are widespread in the study area but are not conducted on drove roads that maintain livestock use (pers. obs.).

Our results also suggest that drove road usage has a positive effect on ant species diversity in adjacent croplands, at least on the edges of these croplands. Some studies have demonstrated that, in warm and dry regions, the presence of ants in croplands facilitates water infiltration, the supply of nitrogen, and the porosity of the soil, which are characteristics associated with the higher production of some cereals (Evans et al. 2011). Therefore, it might be expected that the presence of a used drove road close to croplands would facilitate physical and chemical changes to the soil, which might favor an increase in the productivity. Future research in croplands adjacent to used and abandoned drove roads would be necessary to test potential effects on productivity-yields and explore if these effects extend beyond the borders of the drove road.

The crop type (vineyard or herbaceous) present in the adjacent matrix of both drove roads did not appear to influence the taxonomic and functional diversity of ants. Changes in vegetation structure that occur in environments with a high percentage of intensive cultivation are considered to be followed by changes in the structure of the faunal community in the given area (Whitford 1997). The lack of differences found in this study might be due to a change in vegetation structure, which has a similar effect on ant populations inhabiting both vineyard and herbaceous crops, causing a reduction of available niches or impacts on the microclimate (Gómez et al. 2003).

Regarding ant functional diversity, our results showed that the FD_{Rao} values in the CDR area were higher compared to the MDR area (although these differences were not as marked as those observed for taxonomic diversity). There were also differences in FD_{Rao} on and adjacent to the drove roads, but not between crops adjacent to the CDR and the MDR. Several empirical studies have demonstrated that functional diversity more often determines ecosystem functioning than species richness (Díaz et al. 2006).

In particular, functional traits have been identified as the key mechanism by which single species and groups of species influence ecosystem properties (de Bello et al. 2010). Functional diversity has been used to detect major ecological impacts associated with land use change, with this functional approach being particularly useful in the absence of species-level knowledge (Hausner et al. 2003; Andersen and Majer 2004). Our results suggest that the drove road used by livestock has a higher potential as a functional reservoir compared to the abandoned drove road. This observed difference might have important implications for ecosystem functioning, and the supply of ecosystem services at the landscape level, and also for coping with disturbances of both natural and anthropogenic origin (Lavorel et al. 2007).

However, caution should be taken with the interpretation of our results, as they are heavily location-dependent, and only applicable to the specific conditions of intensive agricultural landscapes in the study area. Under different ecological conditions, drove roads might have different effects on ant diversity, probably related with the characteristics of the surrounding matrix. For example, Azcárate et al. (2013) found that drove roads increase ant diversity in forest landscapes, but exert little or no effect in open environments (rangelands or extensive traditionally managed croplands). Therefore, additional studies about the effect of drove roads on ant diversity at a local scale are required to objectively inform land management at regional or larger spatial scales.

Policy and management implications

Changes in land use are among the main causes of biodiversity loss in Mediterranean ecosystems (Sala et al. 2000). In particular, agriculture intensification has affected the biodiversity of many insect species (Tscharntke et al. 2005); yet, the effects on ant communities remain poorly understood (de Bruyn 1999). Some studies using ants as bioindicators in Australia showed that the main cause of biodiversity loss is agriculture intensification (Majer and Beeston 1996). Moreover, agricultural practices that alter the species composition and/or reduce biodiversity, in agricultural systems and other nonagricultural systems, have a negative impact on ecosystem services (Tilman et al. 2002). This phenomenon arises because the capacity of these systems to provide services is highly dependent on the number of species present (Loreau et al. 2001).

Ants have been widely demonstrated to serve as robust ecological indicators (Andersen and Majer 2004). For instance, the extent of change in ant assemblages may be used as an indicator of broader changes in ecosystems integrity (Andersen et al. 2004). Our study shows that, in a highly disturbed matrix of intensive agricultural fields, a well-preserved drove road with livestock use is associated with higher ant species richness and higher ant functional diversity compared to an abandoned drove road. This observation might have potential implications on ecosystem function and overall biodiversity conservation at a landscape scale. It could be argued that the observed higher species richness is simply a consequence of the presence of opportunistic or common species, which would lower its interest from a species-level conservation perspective. However, it should be noted that, in this case-study, the observed increase was not only due to the presence of generalist/opportunistic species, but also due to the presence of specialist species (see Fig. 4). Although there is no published information available about the status of regional ant fauna, when taking the 1º x 1º grid cells of the Iberian Peninsula as an indicator (www.hormigas.org), we found that seven of the species recorded in the CDR have been recorded in less than 25 % of the cells, for only three of the species found in the MDR. In any case, future research with a species-level approach would be of high interest to fill this knowledge gap and complement our results regarding the conservation relevance of drove roads for ants.

At a larger scale, spatially complex systems (in terms of structural complexity and spatial heterogeneity of vegetation) often tend to exhibit greater species richness (Mac-Arthur 1972). In this case, drove roads are diversifying features that increase habitat heterogeneity at the landscape level, acting as ecological corridors and biodiversity reservoirs (Manzano and Malo 2006; Coughenour 2007; Azcárate et al. 2012), particularly within a matrix of highly transformed, intensive agricultural landscapes. Transhumant livestock movements and the presence of extensive drove road networks are also responsible for the maintenance of critical ecosystem functions and services (González et al. 2012; Carmona et al. 2013). In the context of the uncertainty that accompanies current patterns of global environmental change, traditional practices, such as transhumance, might contribute toward safeguarding multifunctional, cultural landscapes of high natural value (Herzog et al. 2005; Oteros-Rozas et al. 2013). Such practices potentially enhance the adaptive capacity of landscapes to cope with climate

variability and increase social-ecological resilience in Mediterranean agroecosystems (Oteros-Rozas et al. 2012b).

Despite the gradual decline of transhumance in recent decades in Mediterranean Spain, opportunities for the recovery of this practice still exist (Fernández-Giménez and Fillat-Estaque 2012; Oteros-Rozas et al. 2013). The presence of a legally protected network of drove roads is the foundation for this potential recovery, and makes Spain a unique case among developed Mediterranean countries. However, this regulation is not always observed by private and/or public users, leading to abuse and misuse, with many drove roads being partially abandoned and absorbed into other land uses; consequently, losing their role as potential biodiversity reservoirs.

Therefore, action is urgently needed that ensures the effective protection of drove roads for their priority function as livestock routes. Moreover, as the maintenance of drove roads is highly dependent on transhumant livestock use, policy measures are also necessary to safeguard the social and economic sustainability of this traditional practice (Herzog et al. 2005; Oteros-Rozas et al. 2013). By dedicating a certain amount of direct payments to ‘‘greening’’, the new CAP reform aims to ensure that European Union farmers deliver environmental and climatic benefits as part of their daily activities. Therefore, the undergoing CAP reform provides a window of opportunity for the development of mechanisms (e.g., payment for ecosystem services schemes, quality labeling, products marketing, etc.) to promote customary practices, such as transhumance, that contribute toward reversing declines in farmland biodiversity throughout Europe.

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Appendix A

Table A1. Biogeophysical characteristics of the area where the Conquense Drove Road (CDR) and the Murciana Drove Road (MDR) are located.

Description of variables	Categories	CDR	MDR
Altitude	Average	745 m	728 m
Precipitation	Average annual	350-700 mm	350-700 mm
Temperature	Average annual	14.2ºC	14.1ºC
Lithology	Sandstones, conglomerates, loam, limestone and evaporites	47%	31%
	Limestone, dolomite and loams	27%	32%
	Gravels, conglomerates, sands and silts	26%	37%
Biogeoclimatic classification (Roselló et al. 1996)	Ecoregion 6 “Manchega”	100%	100%
Fitoclimates classification (Allue 1990)	IV(VI)1 (“Mancha”)	100%	99.86%
	IV3 (“Interior drylands”)	0%	0.14%
WWF (Olson and Dinerstein 2002)	Iberian sclerophyllous and semi-deciduous forests	100%	100%
Millennium Ecosystems Assessment of Spain classification (EME 2011)	Agroecosystems	84%	85%
	Forest and sclerophyllous shrublands	15%	14%
	Urban areas	1%	1%
Landscape classification (Mata and Sanz 2002)	Plainlands of the southern plateau and its borders	100%	80%
	Wastelands of the southern plateau	0%	20%

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Apendix B

Table B1. UTM coordinates (datum WGS84) of the 32 sampling units in the Conquense Drove Road (CDR) and the Murciana Drove Road (MDR).

ID	Drove Road	Type of adjacent crop	UTM Coordinates	
			X	Y
CV1	CDR	Vineyard	528960	4361951
CH1	CDR	Herbaceous	528700	4361266
CV2	CDR	Vineyard	528164	4360692
CH2	CDR	Herbaceous	527994	4360506
CV3	CDR	Vineyard	527881	4360386
CH3	CDR	Herbaceous	527672	4360153
CH4	CDR	Herbaceous	527157	4359587
CV4	CDR	Vineyard	526866	4359380
CV5	CDR	Vineyard	525909	4358497
CV6	CDR	Vineyard	525282	4357712
CV7	CDR	Vineyard	523579	4356580
CH5	CDR	Herbaceous	523232	4356477
CV8	CDR	Vineyard	523364	4356486
CH6	CDR	Herbaceous	520112	4355339
CH7	CDR	Herbaceous	516357	4352420
CH8	CDR	Herbaceous	515606	4350606
MV1	MDR	Vineyard	542120	4354923
MH1	MDR	Herbaceous	542101	4354840
MH2	MDR	Herbaceous	542755	4354296
MV2	MDR	Vineyard	542817	4354053
MV3	MDR	Vineyard	542928	4353896
MV4	MDR	Vineyard	542986	4353945
MH3	MDR	Herbaceous	543036	4353753

MV5	MDR	Vineyard	543094	4353802
MH4	MDR	Herbaceous	543232	4353648
MH5	MDR	Herbaceous	543397	4353483
MH6	MDR	Herbaceous	543343	4353427
MH7	MDR	Herbaceous	543552	4353319
MV6	MDR	Vineyard	543505	4353262
MV7	MDR	Vineyard	543782	4352912
MH8	MDR	Herbaceous	543941	4352776
MV8	MDR	Vineyard	544477	4351900

Apendix C. Images of the Conquense Drove Road in the cropland matrix.

Capítulo 2.4

Diversidad y abundancia de abejas en una vía pecuaria y su impacto sobre la polinización y producción de semillas en campos de girasol adyacentes

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2.4 Bee diversity and abundance in a livestock drove road and its impact on pollination and seed set in adjacent sunflower fields

Highlights

- Livestock drove roads in intensive agricultural areas act as reservoirs of wild bees.
- Wild bee visitation to sunflower fields was higher near drove roads.
- Wild bee visitation had a significant positive effect on sunflower seed set.
- Increased seed set near the drove road was not related to honey bee visitation.

Abstract

Natural and semi-natural habitats within agricultural landscapes provide food and nesting resources for wild bees, thus promoting crop pollination services. In central Spain, a large network of drove roads (DRs) crosses extensive areas of intensive agricultural fields. DRs are tracks (20–75 m wide) with semi-natural vegetation, protected for their priority function of transhumant livestock herding. In this study, we analyse the bee community of one of the main Spanish DRs, and evaluate its effects on flower visitation and seed set in adjacent sunflower fields. We used pan traps to assess bee abundance and richness at 13 sites along the DR and in adjacent sunflower fields at 10, 75 and 150 m from the DR. We also conducted visual counts to assess visitation rates to sunflower heads and measured seed set. Wild bee abundance and richness were significantly higher in the DR than in sunflower fields; but there were no significant differences among distances within sunflower fields. Honey bee abundance did not differ between the DR and sunflower fields. Wild bee visitation to sunflower heads was higher at 10 m compared to 75 and 150 m from the DR, but differences in honey bee visitation were non-significant. Sunflower seed set was significantly higher at 10 m compared to 75 and 150 m, and was associated with wild bee abundance, but not with honey bee abundance. Our results show that livestock DRs act as reservoirs of wild bee diversity within intensive agricultural matrices, enhancing wild bee visitation and seed set in adjacent sunflower crops.

Keywords: ecosystem services, pollinators, sunflower, livestock transhumance, wild bees

2.4.1 Introduction

Land use intensification usually causes declines in species diversity (Batáry et al., 2011), impacting both ecosystem functioning (Flynn et al., 2009) and ecosystem services (Millennium Ecosystem Assessment, 2005). In particular, agricultural land use intensification has had a noticeable impact on insect pollinators (Connelly et al., 2015; Kennedy et al., 2013), because it typically reduces floral and nesting resources (Le Féon et al., 2010).

Pollination services provided by insects contribute to the productivity of >75% of the world's crop species (Klein et al., 2007). The global value of pollinator-dependent crops has been estimated annually at US$ 235-577 billion (IPBES, 2016). Thus, pollinator decline could cause a sharp reduction in crop yields (Garibaldi et al., 2009; Richards, 2001).

Bees (Apiformes) are the most important pollinator group in most geographical regions (Potts et al., 2010). Although many crops are pollinated with managed honey bees (Apis mellifera), an increasing number of studies have shown that pollination and yields are often enhanced by wild pollinators, even in the presence of honey bees (Breeze et al., 2011; Garibaldi et al., 2013; Greenleaf and Kremen, 2006). Thus, wild bee communities provide insurance against honey bee scarcity (Kremen et al., 2002), with their pollination services potentially exceeding those provided by honey bees (Garibaldi et al., 2013; Winfree et al., 2007).

To enhance and maintain the pollination service, environments favourable to wild bees (including floral and nesting resources, as well as low pesticide pressure) are needed within agricultural landscapes (Ricketts et al., 2008). Because pollinator diversity is often associated with flower diversity (Roulston and Goodell, 2011), habitats with high floristic diversity are expected to provide better pollination services to adjacent croplands (Garibaldi et al., 2011; 2013; 2016).

In particular, in intensive agricultural landscapes, well-connected remnant patches of natural and semi-natural habitat may act as reservoirs of biodiversity (Geslin et al. 2016; Hendrickx et al., 2007; Hevia et al., 2013), and as important providers of several ecosystem services (Carvalheiro et al., 2011; Tscharntke et al., 2005). As central place foragers, wild bees nesting in these habitats may pollinate crops within their foraging

range (Ricketts, 2004). Therefore, the spatial scale that affects agricultural production is determined by foraging distance (Greenleaf et al., 2007).

In the Mediterranean region of Spain, many areas of intensive agriculture are crossed by livestock drove roads (DRs), which represent a highly conspicuous diversifying feature within the agricultural landscape (see Appendix A). DRs are long tracks used for transhumance, an ancient customary practice involving the migration of livestock between summer and winter pasturelands. Because DRs are used for short periods of time, they harbour an important vegetation cover. Plant composition is strongly influenced by seasonal fertilisation and grazing, with many species of entomophilous plants being present year-round, even in the driest summer months (Appendix B). DRs are an important feature of the landscape in Spain (cañadas; Oteros-Rozas et al., 2012) and other countries, including Australia (stock routes, Lentini et al., 2011), France (drailles; Biber, 2010) and Italy (tratturi; Di Martino et al., 2006). Corridors for transhumance have also been described in several regions of Africa (Niamir-Fuller, 1999), central Asia (Fernandez-Gimenez and Le Febre, 2006) and South America (Stewart et al., 1976), although these livestock routes are seldom officially demarcated.

According to Merino and Alier (2004), the Spanish network of DRs includes ca. 125.000 km of 20–75 m wide tracks, and occupies about 0.8% of the national territory. Importantly, Spanish DRs are legally protected for livestock movement (Drove Roads Act from 1995). Previous studies have shown that DRs serve as important reservoirs of both plants (Azcárate et al., 2013a) and ants (Azcárate et al., 2013b; Hevia et al., 2013). In addition, as other semi-natural habitats in agricultural environments that act as reservoirs of pollinators (Bailey et al., 2014), DRs provide areas of untilled bare ground suitable for ground-nesting bees. DRs also contribute to the provision of other ecosystem services, such as seed dispersal and soil fertility (Acín-Carrera et al., 2013; Manzano and Malo, 2006; Oteros-Rozas et al., 2012).

In central Spain, livestock DRs that still remain in use cross important areas of intensive sunflower farming. Sunflower (Helianthus annuus) is one of the most important worldwide sources of oil for human consumption. According to Eurostat (2014), sunflower seed crops in Europe cover almost 4.2 million ha, with an estimated annual production of ca. 9.2 million tonnes. The sunflower inflorescence is a capitulum or head, characteristic of the Compositae family, containing between 1,000 and 2,000 individual sessile protandrous florets. Florets within a head open from the periphery

inwards. Each sunflower head flowers for about 6-10 days. A crop flowers for about 3-5 weeks, depending on local conditions (Free, 1993).

Sunflower plants are highly dependent on pollinators for seed production. Although honey bees are usually the main flower visitors, wild bees have often been found to be more effective pollinators (Free, 1993). Wild plants that grow along sunflower field margins act as important pollen/nectar sources for wild bees and other pollinators (Sabatino et al., 2010; Sáez et al., 2012). In addition to their direct positive effect on sunflower pollination, wild bees have been found to have an indirect effect mediated by interspecific behavioural interactions with honey bees, whereby the sunflower pollination efficiency of honey bees is enhanced when wild bees are present (Greenleaf and Kremen, 2006).

In this study, we aim to (a) evaluate the bee community of a major livestock DR crossing a highly transformed agricultural matrix, and (b) explore the potential influence of the DR bee community on pollination services in adjacent, intensively farmed, sunflower fields. We predict that (1) DRs act as reservoirs of wild bees, (2) wild bee abundance and richness in adjacent sunflower fields decreases with distance from DRs, and (3) sunflower seed set decreases with distance from DRs and increases with increasing wild bee abundance. Our results are expected to provide new insights on pollination services and seed production in intensively farmed sunflower fields.

2.4.2 Material and methods

Study area

The study site is a quite homogeneous agricultural landscape in the Autonomous Community of Castilla-La Mancha (Spain) that extends across the municipalities of Altarejos, San Lorenzo de la Parrilla, Belmontejo, Cervera del Llano, Villalgordo del Marquesado and Villar de la Encina (Fig. 1). The area is a flat plateau (altitude ranging between 830 m and 900 m above sea level), and is characterised by a continental Mediterranean climate with severe summer droughts (mean annual precipitation: 531 mm; mean annual temperature: 13.5 ºC). The lithology is dominated by loams, sandstones and clays from the Miocene. The landscape is mainly composed of non-irrigated cereals and oilseed sunflowers (linoleic variety) that are cultivated under a

rotation regime. These crops are farmed intensively, including the use of sulfonylurea herbicides and various fertilizers. Honey bee hives from other parts of the country are customarily brought to the sunflower fields in July–August to enhance pollination. No bee hive was present in any of our sampling fields but we detected three hive groups in neighbouring semi-natural areas.

The study area is crossed by the Cañada Real Conquense, one of the few major DRs (c.a. 410 km long) that are still in use in Spain. Each year, some 8,900 sheep and 250 cows walk this DR twice between the summering pasturelands in Montes Universales and Serranía de Cuenca (Teruel, Cuenca and Guadalajara provinces), and the southern wintering dehesas of Sierra Morena (Jaén and Ciudad Real provinces) (Fig. 2.4.1; Oteros-Rozas et al., 2012).

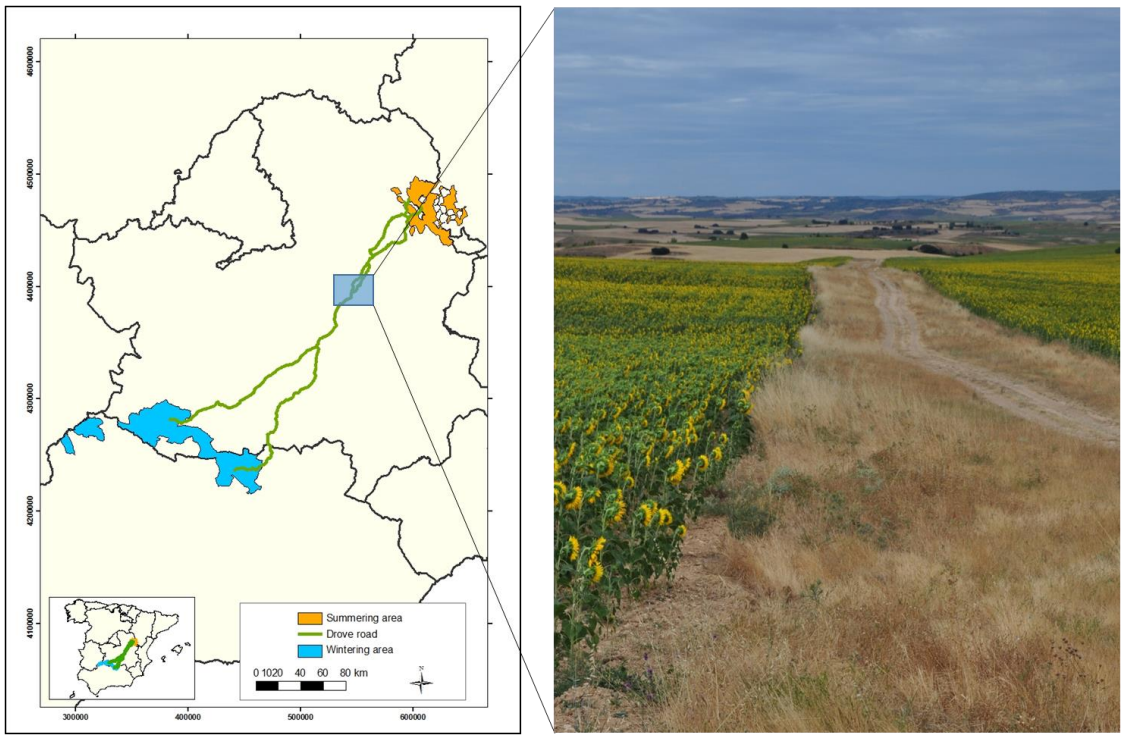

Fig. 2.4.1 Location map of the *Conquense* Drove Road with a photograph of the study area.

Sampling design and data collection

We established 13 sampling sites along a 32-km section of the DR. Sampling sites were selected so that (a) they were separated from each other by at least 1 km, and (b) they were located more than 1 km away from any other natural or semi-natural area (patches

of forest, scrublands, wetlands) potentially harbouring a rich pollinator community. The 1 km distance was chosen because most solitary bees appear to forage within a range of 500 m (Gathmann and Tscharntke, 2002; Zurbuchen et al., 2010). All the fields sampled were planted with the same sunflower linoleic variety (P64LE19).

Bee community sampling

We used pan traps to survey the bee community at the 13 sites. Pan trapping is a good methodology to standardise sampling effort, and is widely used in studies comparing pollinator communities across different sites and environments (Southwood and Henderson, 2000; Westphal et al., 2008). As with any other sampling method, pan trapping has some limitations. Namely, pan traps have been found to underestimate bee richness (Popic et al., 2013), to undersample bumblebees and honey bees (Roulston et al., 2007), and to provide an incomplete measure of flower visitation frequencies (Westphal et al., 2008).

At each site, we established four sampling levels, one on the drove road itself (DR) and three within the adjacent sunflower field at 10, 75 and 150 m from the DR (Fig. 2.4.2). At each level, we set up three pan trap stations separated by 10 m. Each station consisted of a metal bar holding three plastic bowls (yellow, white and blue, respectively) painted with UV-reflective paint to attract flower-visiting insects (Toler et al., 2005; Westphal et al., 2008). Pan traps were held at the same height as the surrounding vegetation (sunflower heads in sunflower fields, wild flowering plants on the DR).

On sampling days, bowls were filled with soapy water to break the surface tension. All sites were sampled twice (in two consecutive days with fair weather) during sunflower peak bloom (between 24 July and 10 August, 2013). Pan traps were operational from sunrise to sunset. Captured bee specimens were dried and pinned for identification in the laboratory.

Each sampling level was characterised by: (a) bee assemblage composition; (b) abundance of honey bees and wild bees (number of captured individuals of each species); and (c) wild bee species richness.

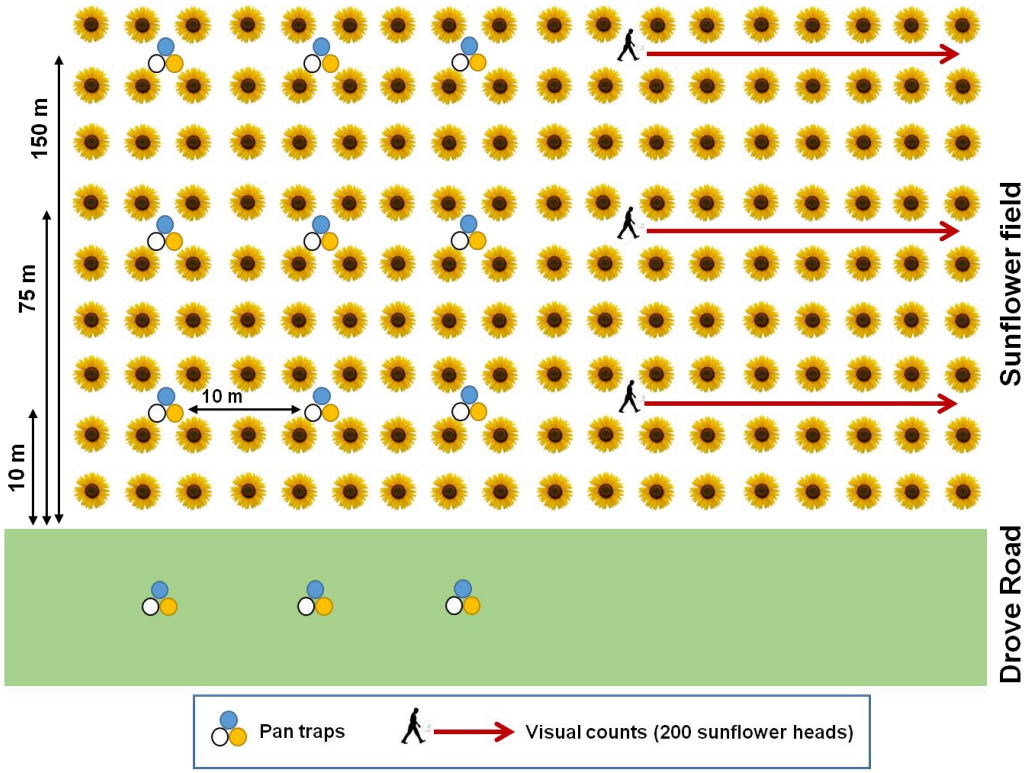

Fig. 2.4.2 Schematic representation of the sampling design.

Bee visitation to sunflower heads

To assess bee visitation to sunflower heads, we worked at 10 of the 13 sites used in the pan trap survey (time constraints did not allow us to sample the remaining three fields). At each site, we established three sampling levels within the sunflower field at 10, 75 and 150 m from the DR. At each level, we made one visual survey, during which an observer walked slowly along a row parallel to the DR and counted all honey bees and wild bees observed collecting pollen and/or nectar from 200 sunflower heads (Fig. 2.4.2). These visual surveys were conducted on the same day as the pan trap survey at each site. All visual surveys were conducted at midday and took approximately 40 min. Each sampling level was characterised by the number of honey bees and wild bees observed visiting sunflower heads.

Seed set

On 3–4 September (when seeds were already mature), we collected eight randomly-selected sunflower heads (capitula) from each sampling level (10, 75 and 150 m) in the

10 sunflower fields that were previously sampled for bee visitation. These capitula were brought to the laboratory where 100 randomly-chosen florets per capitulum were analysed for the presence or absence of seed. Each sampling level was characterised by the mean sunflower seed set (number of florets that produced seed).

Data analysis

To simplify bee species composition to fewer dimensions and facilitate interpretation, sampling levels were organised with a non-metric multidimensional scaling (NMDS) based on Euclidean distances. To detect potential differences in bee composition among levels (DR, 10, 75, and 150 m within the sunflower fields), the position of data points in each of the two axes of the NMDS was analysed with a MANOVA test, using sampling level as a within-subject factor.

We built Generalized Linear Mixed Models (GLMM) to test the effect of the distance from the DR on the various response variables (Bolker et al., 2009). For honey bee and wild bee abundance, wild bee species richness, and honey bee and wild bee visitation, we performed linear mixed models (after data normalisation) using restricted maximum likelihood (REML), with distance from the DR as explanatory variable and site as a random factor. Tukey's HSD tests were then used for post-hoc comparisons. For seed set, the only variable that could not be normalised, we performed a GLMM using a Poisson distribution, with log link function.

Finally, we built another GLMM (Poisson distribution, with log link function) using seed set as the response variable, and honey bee visitation, wild bee visitation, and their interaction as explanatory variables, with site as a random factor. Model selection was based on Akaike's information criterion (Akaike, 1973). Model validity was checked by visual examination of residual plots and by assessment of dispersion parameters. All analyses were performed with XLSTAT 2016 (Addinsoft) and R (v.3.3.3.; R Core Team, 2015).

2.4.3 Results

Bee assemblages

We captured a total of 511 honey bees and 1,224 wild bees (representing 68 species) in the pan traps (Table 2.4.1). *Lasioglossum* was, by far, the most abundant genus in our samples, representing more than 88% of all wild bees that were captured. The NMDS and subsequent MANOVA of bee species composition revealed no differences among the four sampling levels (DR and each of the 3 sunflower distances) (Wilks' Lambda; $F = 0.162$; $P > 0.05$; stress = 0.351).

Honey bee abundance did not significantly differ between the DR and any of the three sunflower distances ($F = 1.490$; $P > 0.05$; Fig. 2.4.3A). In contrast, wild bee abundance varied across sampling levels ($F = 11.934$; $P < 0.001$), being significantly higher on the DR (Tukey tests; $P < 0.05$). No differences were found among the three sunflower distances (Fig. 2.4.3B). Similarly, wild bee species richness varied significantly across sampling levels ($F = 8.076$; $P < 0.001$; Fig. 2.4.4). The highest species richness was detected in traps located on the DR (Tukey tests; $P < 0.05$), and no differences were detected among the three sunflower distances (Fig. 2.4.4).

Table 2.4.1. Wild bee species found on the drove road (DR) and at 10, 75 and 150 m from the DR in adjacent sunflower fields.

Species	DR	10 m	75 m	150 m
Amegilla albigena	X			X
Amegilla fasciata	X			
Andrena spp1	X		X	X
Andrena spp2	X			
Andrena spp3	X	X		X
Andrena albopunctata			X	X
Ceratina chalybea	X			
Ceratina dentiventris		X		
Chelostoma spp1			X	
Eucera elongatula	X	X		X
Eucera obliterata			X	
Eucera (Synhalonia) rufa	X		X	
Eucera taurica		X		
Eucera (Synhalonia) tricincta				X
Halictus gemmeus	X			
Halictus quadricinctus	X		X	
Halictus scabiosae		X		
Halictus sexcinctus	X			
Halictus smaragdulus	X	X	X	X
Halictus subauratus	X	X		
Halictus tetrazonius	X	X	X	X
Halictus vestitus	X		X	
Heliophila fulvodimidiata			X	
Hoplitis sp1	X	X	X	X
Hoplitis sp2		X	X	X

Species	DR	10 m	75 m	150 m
Hoplitis cristatula			X	
Hylaeus sp1	X		X	X
Lasioglossum (Evylaeus) sp1	X	X	X	X
Lasioglossum (Evylaeus) sp2	X	X	X	X
Lasioglossum (Evylaeus) sp3	X			
Lasioglossum (Evylaeus) sp4			X	
Lasioglossum (Evylaeus) sp5	X		X	
Lasioglossum (Evylaeus) sp6	X			
Lasioglossum (Evylaeus) sp7	X	X	X	X
Lasioglossum (Evylaeus) sp8	X		X	X
Lasioglossum (Evylaeus) sp9	X	X	X	X
Lasioglossum (Evylaeus) nigripes			X	
Lasioglossum (Lasioglossum) sp1	X	X	X	
Lasioglossum (Lasioglossum) sp2	X	X	X	X
Lasioglossum (Lasioglossum) sp3	X			X
Lasioglossum (Lasioglossum) sp4		X		
Lasioglossum albocinctum	X	X	X	X
Lasioglossum clypeare	X	X		X
Lasioglossum discum	X	X	X	X
Lasioglossum glabriusculum	X	X	X	X
Lasioglossum griseolum	X	X	X	X
Lasioglossum interruptum	X	X	X	X
Lasioglossum malachurum	X	X	X	X
Lasioglossum morio		X	X	X
Lasioglossum puncticolle	X	X	X	X
Lasioglossum semilucens	X			
Lasioglossum subhirtum	X			X
Lasioglossum transitorium	X		X	X
Lithurgus chrysurus	X			
Megachile albisecta	X	X		
Nomada sp1	X			
Osmia signata	X			
Panurgus siculus				X
Sphecodes sp1		X		
Sphecodes sp2				X
Tetraloniella dentata	X			X
Tetraloniella nana	X	X	X	
Xylocopa cantabrita	X			X

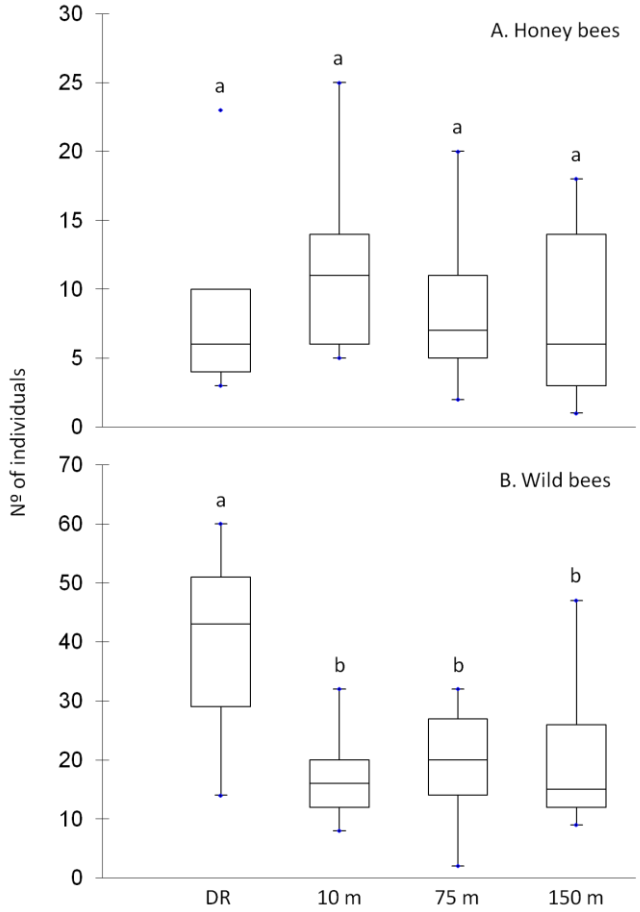

Fig. 2.4.3 Number of honey bees (A) and wild bees (B) captured in pan trap stations on the drove road (DR) and in adjacent sunflower fields at 10, 75 and 150 m from the DR. Different letters indicate significant differences ($P < 0.05$).

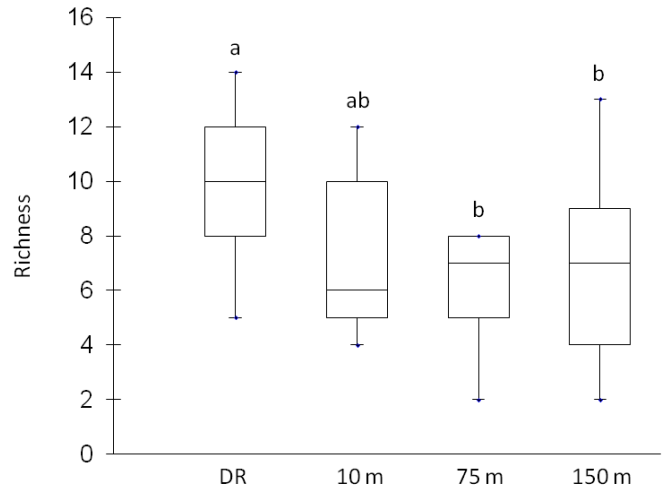

Fig. 2.4.4 Wild bee species richness per sampling level on the drove road (DR) and in adjacent sunflower fields at 10, 75 and 150 m from the DR. Different letters indicate significant differences ($P < 0.05$).

Bee visitation

We recorded a total of 2,014 honey bees and 92 wild bees visiting sunflower heads. Visual counts of honey bees were not significantly different across levels ($F = 2.786$; $P > 0.05$; Fig. 2.4.5A). On the other hand, visual counts of wild bees significantly decreased with distance from the DR ($F = 52.908$; $P < 0.001$). The greatest number of wild bees was observed at 10 m from the DR and the lowest at 150m (Tukey tests; $P < 0.05$; Fig. 2.4.5B).

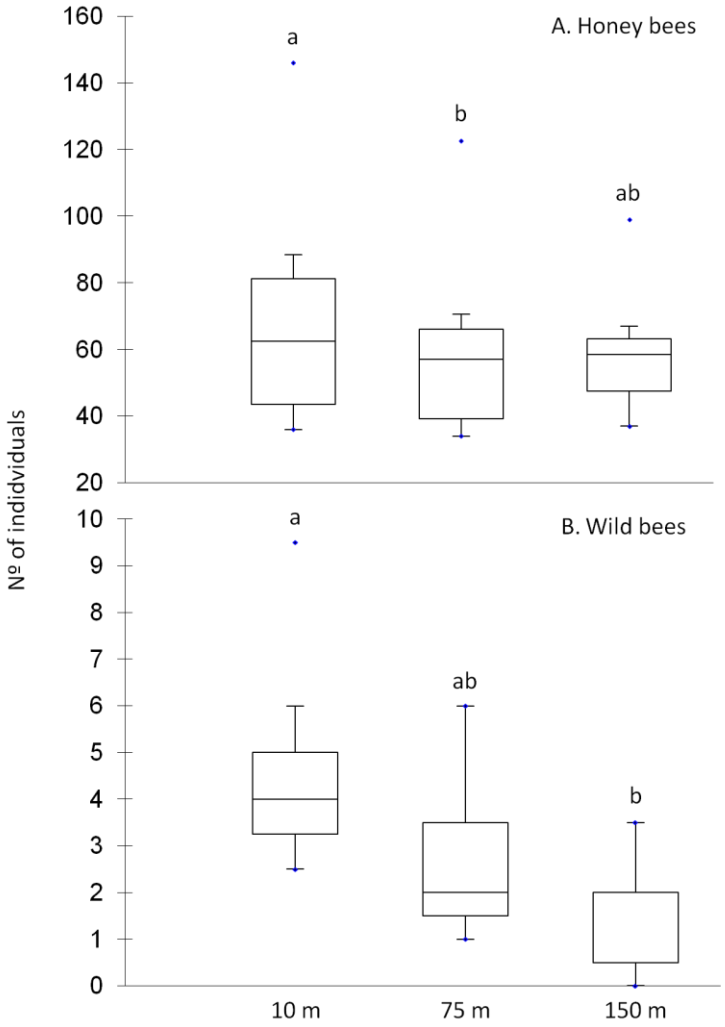

Fig. 2.4.5 Number of honey bees (A) and wild bees (B) observed visiting sunflower heads at 10, 75 and 150 m from the drove road. The median of the 150 m-box plot overlaps with the lower quartile. Different letters indicate significant differences ($P < 0.05$).

Seed set

Seed set varied significantly among sampling levels ($\chi 2 = 8.500$; $P < 0.05$), being higher at 10 m from the DR compared to 75 and 150 m ($P < 0.05$; Fig. 2.4.6). The most parsimonious GLMM (AIC = 210.2) included wild bee and honey bee visitation as predictors of sunflower seed set (Table 2.4.2); but not the interaction between wild bee and honey bee visitation; however, only wild bee visitation had a significant effect on seed set ($\chi 2 = 12.528$; $P < 0.001$).

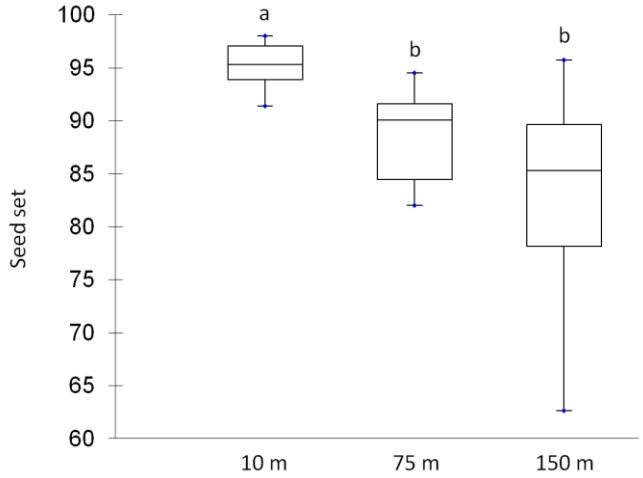

Fig. 2.4.6 Seed set in sunflower heads at 10, 75 and 150 m from the drove road. Different letters indicate significant differences ($P < 0.05$).

Table 2.4.2 Results of the most parsimonious GLMM with seed set (arcsin-square-root transformed) as the response variable, and wild bee and honey bee visitation (lntransformed) as explanatory variables.

Response variable	Explanatory variable	Degr. of freedom	MS	F	P
Seed set	Intercept	1	91,8488	1,69886	0,208840
	Ln Wild bees	1	882,1911	23,56313	**0,000127**
	Ln Honey bees	1	5,5043	0,21334	0,649693
	Transect	9	25,7569	0,71504	0,689178

2.4.4 Discussion

Drove roads as important landscape features that influence bee assemblages

Our results show that wild bee abundance and species richness were higher in the DR compared to adjacent sunflower fields. Yet, species composition was similar in both habitat types. In other words, sunflower assemblages may be considered a poorer version of DR assemblages, suggesting that DRs act as reservoirs of wild bee diversity. This effect is important in a landscape dominated by sunflower fields which only provide pollen/nectar during a brief period of time, and cereal crops which provide no valuable food resources for bees. In contrast to wild bees, the abundance of honey bees was similar in the DR and sunflower fields. This phenomenon might be explained by the location and spatial arrangement of managed hives (Cunningham and Le Feuvre, 2013; Cunningham et al., 2015), and the longer flight range (several kilometres) of honey bee foragers (Visscher and Seeley, 1982).

Many studies have evaluated the role of field margins, hedgerows, flower strips and road margins within monoculture landscapes in pollinator conservation (Blaauw and Isaacs, 2014; Morandin and Kremen, 2013). These agro-environmental structures provide diverse pollen/nectar resources and nesting sites; thus, promoting crop pollination services (Garibaldi et al., 2014; Mandelik et al., 2012; Nicholls and Altieri, 2012; Sáez et al., 2014; Scriven et al., 2013). However, as far as we know, there are no previous studies that address the importance of livestock DRs as reservoirs of wild bee diversity and enhancers of pollination services in adjacent fields.

DRs have some unique characteristics that make them particularly important from a pollinator conservation perspective. First, DRs are much wider than regular field margins; thus, providing greater continuous cover of bee-suitable habitat. Second, DRs harbour a unique and more diverse flora compared to other agro-environmental structures, such as managed field margins, hedgerows and flower strips. DR plant communities are strongly modelled by the seasonal grazing of transhumant herds (Azcárate et al., 2013); thus, providing pollen/nectar sources that are not found in other agro-environmental structures. Although the plant species composition of DRs is dominated by terophytes that die in late spring, many perennials and longer-lived annuals bloom during the dry summer months (52 plant species flowering in August,

see Appendix B). An uninterrupted period of diverse pollen/nectar sources is important for maintaining wild bee populations that remain active through the summer, especially when wild bee populations fluctuate widely, with several years being required for them to colonise habitats (Williams et al., 2001). Third, DRs are important for landscape connectivity (Manzano and Malo, 2006; González et al., 2012). Connectivity has been positively linked to biodiversity, ecosystem function (Fahrig et al., 2015; Rodriguez Gonzalez et al., 2008) and the supply of various ecosystem services (Tscharntke et al., 2005), including crop pollination (Mitchell et al., 2013). In particular, the Conquense DR is an ideal example of an ecological corridor that connects natural habitats (e.g., coniferous forests in summering areas, with isolated Mediterranean forest patches and holm oak *dehesas* in wintering areas) across an intensive cropland matrix (González et al., 2012; Oteros-Rozas et al., 2012).

Effects of drove roads on pollination services in adjacent crops

Both wild bee visitation and sunflower seed set decreased with increasing distance from the DR. Contrarily, honey bee visitation was similar across sampling levels. The GLMM results also showed that only wild bee visitation had a significant effect on seed set. That is, wild bees significantly contributed to sunflower seed set despite honey bee visitation being an order of magnitude higher. Previous studies have also shown wild pollinator abundance and diversity to be directly related to pollination efficiency and crop production (Carvalheiro et al., 2011; Jauker et al., 2012; Kremen et al., 2012; Nayak et al., 2015; Petersen et al., 2013). Our findings are consistent with previous studies on sunflowers reporting that wild bees significantly contribute to seed yields (Carvalheiro et al., 2011; Sáez et al., 2012); however, other studies on sunflowers have not found wild bee contribution to be significant (Pisanty et al., 2014).

Although our model did not show a significant effect of the interaction between wild bee and honey bee visitation on seed set, previous studies reported that sunflower pollination was enhanced by interspecific interactions between wild bees and honey bees in hybrid sunflower cultivars. For example, DeGrandi-Hoffman and Watkins (2000) found that honey bees carried more sunflower pollen on their bodies in fields where wild bees were more abundant, and Greenleaf and Kremen (2006) documented the existence of interspecific behavioral interactions that increase the frequency of

honey bee pollen transfers from male to female plants, resulting in a two-fold increase in the per-visit effectiveness of honey bees. Two mechanisms are involved in this effect. First, wild bee males searching for mates may physically interfere with honey bees, causing them to fly away and thus increasing the probability that a honey bee visiting a male-fertile sunflower row lands on a male-sterile sunflower row. Second, nectar-collecting honey bees, which mostly visit male-sterile sunflower heads, may contribute to pollination by spreading clumps of pollen deposited on these heads by wild bees (Greenleaf and Kremen, 2006).

Our results show that the DR had an important influence on wild bee visitation and seed set in sunflowers, but the range of this effect was limited, with significant effects declining from 10 to 75 m from the DR. Although foraging distances of most wild bees have been estimated to be well beyond 100 m (Gathmann and Tscharntke, 2002; Greenleaf et al., 2006; Guédot et al., 2006; Zurbuchen et al., 2010), actual foraging distances are often within tens of meters in flowering crop fields, especially when plants are in full bloom with abundant pollen/nectar resources (Biddinger et al., 2013; Vicens and Bosch, 2000). Yet, considering only a band of 10 m of sunflower fields adjacent to the DR, we estimate that each Km of DR contributes, on average, to an 11% (95% CI= 5.4% – 13.8%) increase in sunflower seed production.

It is worth noting that the coefficients of variation (CV) of abundance of sunflower-visiting wild bees and of seed set, both increase with distance from the DR (2-fold increase for wild bees and 2.5-fold increase for seed set from 10 to 150 m). This is important because variation in pollen delivery has been associated to reduced yield mean and stability in pollinator-dependent crops (Garibaldi et al., 2011). Finally, although our results show a significant influence of wild bee visitation on seed set, the effect of other factors associated with distance from the DR cannot be completely ruled out. Other ecosystems services potentially provided by DRs (e.g., improved pest control, fertilization due to livestock droppings), or simply a border effect could also positively affect seed set in the sunflowers growing close to the DR.

Management implications in times of bee diversity declines

Maintaining diverse bee communities is essential to ensure adequate pollination services (Kremen et al., 2002). Thus, the identification of key factors that enhance landscape-

wide wild bee communities is important for the long-term sustainable management of agroecosystems (Westphal et al., 2003). Natural and semi-natural habitats fulfil an essential role in sustaining functionally diverse wild pollinator communities. Thus, to preserve and support bee populations in Europe, the preservation of flower-rich semi-natural habitats should be promoted (Le Féon et al., 2010).

DRs act as diversifying features that increase habitat heterogeneity at the landscape level, also serving as ecological corridors and diversity reservoirs (Azcárate et al., 2013b; Hevia et al., 2013; Manzano and Malo, 2006). Consequently, the conservation value of DRs has been widely recognised in Spain (Gómez-Sal and Lorente, 2004; Mangas-Navas, 2004), resulting in their being granted legal protection for the priority use of herding animals. Our study extends our understanding on the role of DRs as unique landscape elements, acting as reservoirs of wild bees, with important repercussions on pollination services in adjacent croplands.

However, the gradual decline of transhumance in recent decades (Fernández-Giménez and Fillat Estaque, 2012) has led to the partial abandonment and transformation of DRs (Oteros-Rozas et al., 2013). Abandoned DRs rapidly lose their role as potential reservoirs of biodiversity because they are transformed or partially absorbed into other land uses (Hevia et al., 2013). Therefore, political action is needed to ensure the effective protection of DRs for their priority function as livestock roads. Given that the maintenance of DRs is highly dependent on transhumant livestock use, policy measures are also required to safeguard the socioeconomic viability of this traditional practice (Herzog et al., 2005; Oteros-Rozas et al., 2013). The new Common Agricultural Policy of the European Union offers a window of opportunity to focus investments towards the efficient delivery of ecosystem services from agricultural lands (Plieninger et al., 2012). Promoting traditional practices, such as livestock transhumance, may contribute towards reversing declines in farmland biodiversity, including pollinators, throughout Mediterranean Europe.

2.4.5 Conclusions

This study shows that a functioning livestock drove road serves as an efficient reservoir of wild bee pollinators in a highly transformed agricultural matrix. Our results suggest that the drove road enhances wild bee visitation to sunflower heads, with a resulting

increase in seed set in areas closer to the drove road, even against a background of high honey bee abundance. To guarantee effective crop pollination, the conservation of natural or semi-natural habitats (such as drove roads) within intensive agricultural landscapes should be prioritized in future agricultural policies.

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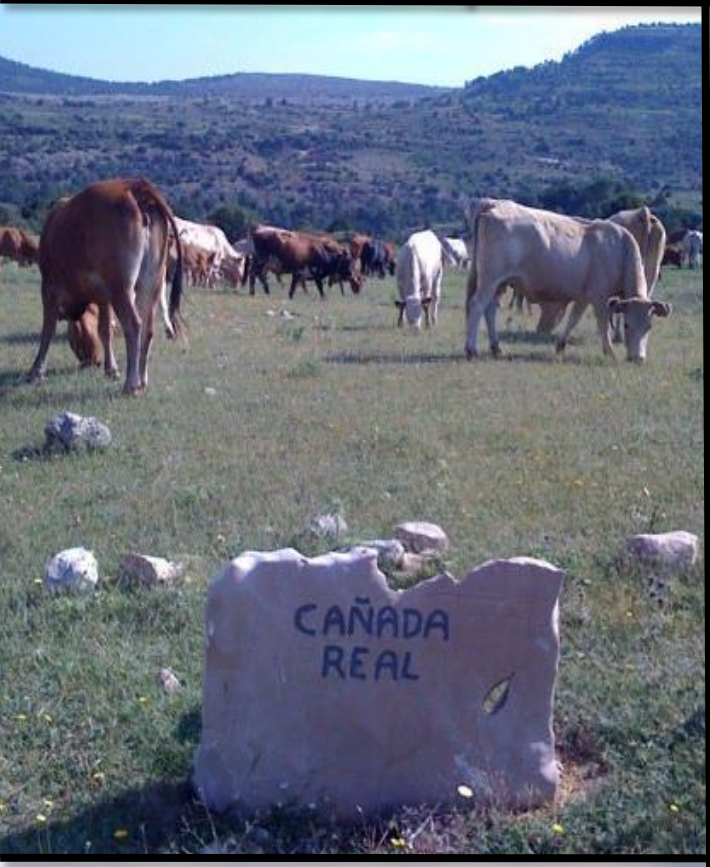
Appendix A
Photographs of the study area

Herd of transhumant sheep moving along the drove road

Herd of transhumant cattle moving along the drove road

Appendix B. Plant species found on the drove road (DR).

Species	Sampling point							
	DR3	DR4	DR5	DR6	DR7	DR8	DR9	DR10
Allium sp.	0	0	0	0	0	6	0	0
Anthemis arvensis	0	0	2	6	0	0	6	2
Atractylis humilis	3	5	3	0	5	0	0	5
Bupleurum fruticescens	5	0	0	0	0	0	0	5
Carlina corymbosa subsp. *hispanica*	6	0	0	0	4	0	0	6
Carthamus lanatus	6	3	4	0	6	4	6	0
Centaurea aspera subsp. *aspera*	0	2	0	0	0	0	0	0
Centaurea aspera subsp. *stenophylla*	1	5	3	0	0	0	0	1
Centaurea calcitrapa	2	0	2	0	3	0	4	0
Centaurea castellanoides	0	0	0	0	0	6	2	2
Centaurea cephalariifolia	0	0	0	0	0	6	6	0
Centaurea melitensis	3	0	0	0	0	0	0	0
Centaurea ornata	3	0	0	0	0	0	0	0
Chondrilla juncea	2	1	6	6	4	6	4	5
Cichorium intybus	0	0	1	0	0	0	0	0
Cirsium arvense	1	0	2	0	0	0	1	6
Cirsium pyrenaicum	0	0	5	0	0	0	0	0
Convolvulus arvensis	1	0	6	6	0	0	1	0
Daucus carota	1	0	1	0	0	1	0	0
Dorycnium pentaphyllum	0	0	2	0	0	0	0	0
Echinops ritro	1	1	1	0	1	2	2	1
Echinops strigosus	0	0	0	1	0	0	1	1
Eryngium campestre	1	4	1	5	5	1	1	1
Eryngium dilatatum	2	0	0	0	0	0	0	0
Euphorbia sp.	0	2	1	0	0	0	0	1
Galium aparine	0	0	1	0	0	0	0	0
Hedysarum boveanum	0	0	0	0	0	0	0	3
Helminthoteca echioides	0	0	0	6	0	0	0	0
Hypericum sp.	0	0	0	0	0	1	0	0
Inula sp.	1	0	0	0	0	0	0	0
Lactuca serriola	1	2	1	1	3	1	2	1
Lavandula latifolia	1	0	1	0	0	0	0	0
Mantisalca salmantica	0	0	3	0	0	0	0	0
Medicago sp.	1	1	1	3	1	2	1	1
Ononis spinosa	1	0	0	0	0	0	0	0
Pallenis spinosa	0	0	0	0	0	3	0	0
Papaver sp.	0	0	0	0	0	1	0	0
Plantago albicans	0	0	0	1	0	1	0	0
Plantago coronupus	0	0	0	0	0	0	1	0
Picnomon acarna	5	1	4	2	6	3	1	6
Reseda lutea	0	1	0	0	0	0	0	0
Satureja intricata	1	2	1	0	0	0	0	0
Scolymus hispanicus	0	2	1	0	1	1	0	0
Xanthium spinosum	0	0	0	0	0	0	1	0
Unknown 1	0	0	0	0	0	0	1	0
Unknown 2	0	1	3	0	0	0	3	1
Unknown 3	0	0	0	0	0	5	0	1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Capítulo 3

Discusión

3.1 Cambio de uso del suelo, biodiversidad y servicios de los ecosistemas: el efecto de la intensificación sobre la conectividad, heterogeneidad y multifuncionalidad de los agroecosistemas mediterráneos

3.2 Los rasgos funcionales como aproximación para entender los vínculos entre los impulsores directos de cambio y los servicios de los ecosistemas: el Santo Grial de la ecología funcional

3.3 Retos futuros para la investigación basada en el marco de los rasgos funcionales de “respuesta y efecto”: desafíos metodológicos y nuevas fronteras

En el actual contexto de Cambio Global, los ecosistemas están expuestos a los efectos de los diferentes impulsores directos de cambio, cuya repercusión varía en función de la escala de análisis utilizada y de los biomas de los que se trate (Sala et al. 2000). Conocer qué impulsores directos de cambio influyen de manera más determinante en la funcionalidad de cada tipo de ecosistema resulta esencial para entender y predecir las consecuencias del Cambio Global, así como plantear y desarrollar posibles estrategias de adaptación (Scheffer et al. 2015). Esta Tesis Doctoral pretende contribuir a aumentar el conocimiento existente sobre los efectos de los impulsores directos de cambio sobre la diversidad (taxonómica y funcional) de distintos grupos de organismos, y su traducción en el suministro de servicios de los ecosistemas.

En línea con los estudios existentes hasta la fecha, los resultados del capítulo 2.1 (que responde al primer objetivo específico de esta Tesis), reflejan claramente que los mayores impactos humanos sobre la biodiversidad de los ecosistemas se han materializado a través de los cambios de usos del suelo (MA 2005; Pereira et al. 2012). Por ello, en las otras tres secciones del capítulo de Resultados (2.2, 2.3, y 2.4) se abordaron los otros dos objetivos específicos de la Tesis, centrados en el análisis de los efectos de los cambios de uso del suelo a través de varios casos de estudio empíricos en agroecosistemas mediterráneos, en los que se exploraron algunas de las relaciones existentes entre usos del suelo con distinto grado de intensificación, la biodiversidad y los servicios de los ecosistemas.

En este capítulo se aborda la Discusión general e integradora de la Tesis, que ha sido estructurada en tres grandes secciones. La primera de ellas (3.1) versa sobre el papel de la intensificación de los usos del suelo y sus efectos sobre la biodiversidad y el suministro de servicios de los ecosistemas. Sobre la base de los casos empíricos desarrollados en esta Tesis, se discuten los principales resultados obtenidos tratando de identificar y describir aquellos factores que actúan de manera significativa en las relaciones complejas exploradas y que pueden contribuir finalmente a la mayor o menor multifuncionalidad de los agroecosistemas mediterráneos.

En la sección 3.2 se realiza un análisis en profundidad sobre el uso de los rasgos funcionales como aproximación para explorar los vínculos entre los impulsores directos de cambio (con el foco puesto especialmente en los cambios de uso del suelo) y los servicios de los ecosistemas. Por una parte, se analizan las ventajas e inconvenientes generales del uso de esta aproximación para la consecución de los objetivos planteados

en este trabajo, con especial énfasis en los aportes que puede brindar este marco respecto al desarrollo de reglas predictivas generales sobre los efectos del Cambio Global en las comunidades biológicas. Asimismo, se discute el papel de la redundancia funcional y sus relaciones con la resiliencia de los ecosistemas.

La sección 3.3 aborda las limitaciones metodológicas identificadas en el uso de los rasgos funcionales como aproximación, planteándose algunas alternativas que puedan dar respuesta a dichas limitaciones. Además, se desarrollan una serie de propuestas en relación a nuevos retos de la investigación en este campo, surgidas a partir de los resultados obtenidos en esta Tesis y la discusión de los mismos con las propuestas recogidas en otras investigaciones previas.

3.1 Cambio de uso del suelo, biodiversidad y servicios de los ecosistemas: el efecto de la intensificación sobre la conectividad, heterogeneidad y multifuncionalidad de los agroecosistemas mediterráneos

El cambio de uso del suelo ha sido identificado como el principal impulsor directo de cambio a escala global (MA 2005). Los cambios de uso del suelo han sido particularmente relevantes en la Europa rural, donde han estado dominados principalmente por dos procesos antagónicos: la intensificación agrícola y el abandono de tierras (Plieninger et al. 2006; Andersen 2010). Los procesos de intensificación agrícola provocan, además de la propia pérdida de hábitat, otros muchos efectos relacionados con la pérdida de conectividad a través de la fragmentación de hábitats o el aumento de los insumos agroquímicos en los hábitats naturales o semi-naturales de las zonas adyacentes (Benton et al. 2002; Oliver y Morecroft 2014).

Los paisajes agrarios tienen una especial relevancia en Europa, ocupando más del 45% de la superficie de la Unión Europea (FAOSFAT 2005; Overmars et al. 2013). En estos paisajes agrarios, los manejos tradicionales del suelo favorecen el mantenimiento de la biodiversidad en muchos agroecosistemas (Bignal y McCracken 2000; Halada et al. 2011), siendo además elementos importantes para los programas de conservación a escalas espaciales más grandes (Tscharntke et al. 2005). Sin embargo, estos tipos tradicionales de uso del suelo han descendido drásticamente en nuestro continente a lo largo de los últimos años (Henle et al. 2008). Actualmente, la intensificación de la

agricultura se presenta como una de las actividades humanas que más afecta negativamente a la diversidad de aves, mamíferos, plantas, insectos, y fauna edáfica (Benton et al. 2002; Tscharntke et al. 2005; Breitbach et al. 2010; Tsiafouli et al. 2014), así como al suministro de servicios de los ecosistemas (Tilman et al. 2002).

Los tres casos de estudio desarrollados en esta Tesis (capítulos 2.2, 2.3, y 2.4) se focalizan principalmente en agroecosistemas expuestos a distintos grados de intensificación relacionados con el manejo de algunos de los cultivos predominantes en la cuenca mediterránea en general, y la Península Ibérica en particular (por ejemplo: girasol, viñedos, u olivares). Los resultados obtenidos acerca del efecto negativo de la intensificación del uso del suelo sobre la diversidad de distintos grupos (vegetación herbácea y leñosa, aves, hormigas y abejas) van en línea con los hallazgos previamente descritos en otros estudios (Flynn et al. 2009).

En concreto, en los capítulos 2.3 y 2.4 se exploró el efecto de las vías pecuarias con uso ganadero trashumante sobre la diversidad de invertebrados (hormigas y abejas) en ambientes de agricultura intensiva. En ambos casos, se observó que los valores de diversidad eran significativamente menores en los cultivos manejados de manera intensiva frente a un hábitat semi-natural como es la vía pecuaria en la zona de estudio. Así, el manejo no intensivo correspondiente a la vía pecuaria se traduce en la presencia de una serie de elementos clave que pueden explicar fácilmente los mayores valores de diversidad de los grupos de invertebrados estudiados.

En primer lugar, la ausencia de insumos químicos (herbicidas, insecticidas, etc.), y alteraciones físicas (arado, paso de maquinaria pesada, etc.), dan lugar a hábitats relativamente poco perturbados en un contexto ampliamente alterado por actividades humanas y que, por tanto, permiten que un mayor número de especies de invertebrados puedan establecerse en dichos hábitats a medio y largo plazo. Por otra parte, los hábitats semi-naturales como la vía pecuaria aumentan la disponibilidad de refugios. Tanto las hormigas como muchas especies de abejas silvestres (así como otra fauna edáfica potencialmente presente en los agroecosistemas) construyen sus nidos en el suelo. El mantenimiento de la estructura del suelo por medio de la vegetación silvestre presente en la vía pecuaria, así como la ausencia de perturbaciones mecánicas derivadas del manejo del suelo en los cultivos, favorecen las condiciones necesarias para mantener los nidos en buenas condiciones. Además, algunas especies de abejas solitarias utilizan tallos de plantas presentes en la vía pecuaria para construir sus nidos. Finalmente, la

disponibilidad de plantas silvestres con flor en la vía pecuaria (favorecida además por la dispersión de semillas llevada a cabo por el ganado trashumante (Manzano y Malo 2006)) puede constituir una fuente de alimento esencial para las abejas silvestres y melíferas, con especial relevancia en las fases de no floración de los cultivos adyacentes.

En cualquier caso, es importante tener en cuenta que entre los agroecosistemas más intensivos y un hábitat semi-natural como una vía pecuaria con actividad trashumante, existe una amplia gama de sistemas de manejo con distintos grados de intensificación. Precisamente con objeto de explorar el efecto de algunos de dichos manejos, se planteó el capítulo 2.2 de la Tesis, cuya zona de estudio presenta cuatro usos del suelo predominantes (de menor a mayor grado de intensificación): monte mediterráneo, dehesa, pinar de repoblación y olivar. Los resultados de este capítulo mostraron que los patrones de diversidad taxonómica y funcional de los grupos de organismos estudiados (vegetación herbácea y leñosa, aves y hormigas) en respuesta a cada intensidad de uso del suelo son altamente complejos, varían con el tipo de organismo, y dependen de la escala espacial utilizada.

En resumen, los resultados de estos tres capítulos muestran que los valores de diversidad (taxonómica y funcional) de varios tipos de organismos difieren cuando se comparan usos del suelo con grados de intensificación marcadamente distintos (es decir, usos con mucha intensificación vs. usos extensivos). Sin embargo, esas diferencias se difuminan en patrones altamente contexto-dependientes cuando se analiza también el efecto de varios usos del suelo con grados de intensificación intermedios.

Como se mencionó anteriormente, altos valores de intensificación de los usos del suelo desencadenan habitualmente una **degradación de la conectividad en el paisaje**, lo que implica también impactos negativos en la biodiversidad (Sala et al. 2000; Huston 2005). Es por ello que en los últimos años se ha puesto de manifiesto la necesidad de priorizar aquellos elementos que actúen como corredores y aumenten la "permeabilidad" en el paisaje (Theobald et al. 2012). En contextos de agricultura intensiva, la conectividad entre hábitats naturales o semi-naturales, así como entre éstos y los cultivos adyacentes y próximos, resulta clave para el movimiento y dispersión de especies animales y vegetales (Tscharntke et al. 2007; Brudvig et al. 2009; Blitzer et al. 2012; Concepcion et al. 2012). En este sentido, las vías pecuarias presentes en dos de las zonas de estudio de

esta Tesis constituyen buenos ejemplos de estructuras capaces de aumentar la conectividad en paisajes agrícolas muy homogéneos y altamente intensificados.

Además, **la heterogeneidad del paisaje** es otro de los factores que pueden ser determinantes en el mantenimiento de la biodiversidad y el suministro de servicios de los ecosistemas en contextos de agricultura intensiva. La "hipótesis de la heterogeneidad del hábitat" es una de las piedras angulares de la Ecología, y asume que los hábitats estructuralmente complejos pueden proporcionar mayor número de nichos y, por tanto, pueden albergar una mayor diversidad de especies (Simpson 1949; MacArthur y Wilson 1967; Lack 1969). Diversos estudios han explorado el efecto de la heterogeneidad de los hábitats sobre la biodiversidad, encontrando que generalmente es la comunidad de plantas la que determina en buena medida la estructura física del hábitat, lo que tiene un efecto significativo sobre las interacciones y distribución de las especies animales (McCoy y Bell 1991; Tews et al. 2004). Por ello, en un contexto con una matriz de usos de suelo altamente transformada como son los paisajes de agricultura intensiva estudiados en este trabajo, los márgenes de los propios campos y de las carreteras, así como setos u otras estructuras con vegetación floral, desempeñan un rol importante en la conservación de la biodiversidad en general, con especial relevancia para los insectos polinizadores (Morandin y Kremen 2013; Blaauw y Isaacs 2014). Esto tiene unas implicaciones muy determinantes en el suministro del servicio de polinización de dichos cultivos, ya que estas estructuras actúan como hábitats semi-naturales que proporcionan lugares de nidificación y recursos de polen y néctar para las abejas (Mandelik et al. 2012; Nicholls y Altieri, 2012; Sáez et al. 2012; Scriven et al. 2013; Garibaldi et al. 2014). En estos paisajes dominados por monocultivos, una vía pecuaria actúa por tanto como un elemento diversificador, con un alto valor natural y cultural (Gómez Sal y González García 2007), que incrementa la conectividad y heterogeneidad del hábitat a nivel de paisaje, y actúa además como corredor y reservorio de biodiversidad (Gómez Sal y Lorente 2004; Manzano y Malo 2006; Coughenour 2008; Azcárate et al. 2012).

Basándonos en los resultados de los capítulos 2.3 y 2.4 de esta Tesis, podemos concluir que la presencia de vías pecuarias bien conservadas en paisajes de agricultura intensiva aumenta los valores de diversidad taxonómica y funcional de invertebrados en las zonas de cultivo adyacentes, favoreciendo además el suministro de algunos servicios de los ecosistemas como la polinización, que tiene efectos directos sobre la producción de

algunos cultivos como el girasol, altamente dependientes de la polinización por parte de abejas silvestres y melíferas.

Nuestros resultados apuntan a que los factores que determinan el efecto de los usos del suelo sobre la biodiversidad y los servicios de los ecosistemas en agroecosistemas mediterráneos son principalmente: el grado de intensificación, la conectividad entre hábitats naturales y/o semi-naturales, y la heterogeneidad del paisaje. Así, en paisajes con una agricultura intensiva predominante, se torna crucial la presencia de estructuras que favorezcan la conectividad y la heterogeneidad del paisaje y contribuyan a crear **agroecosistemas multifuncionales** en aras de mantener mayores valores de biodiversidad como base para el suministro de diversos servicios de los ecosistemas.

La **multifuncionalidad de los ecosistemas,** entendida en último término como la producción simultánea de múltiples funciones y servicios de los ecosistemas (Hector y Bagchi 2007) viene determinada por diferentes componentes de las comunidades biológicas, tales como la diversidad taxonómica, la identidad funcional y la diversidad funcional (Hooper y Vitousek 1997; Díaz et al. 2007). Así, una de las cuestiones más relevantes para la comprensión de los procesos ecológicos son los efectos y las contribuciones específicas de cada componente de la biodiversidad a la multifuncionalidad de los ecosistemas (Mouillot et al. 2011).

Los efectos sobre las funciones y servicios de los ecosistemas tanto de las especies individuales (Gamfeldt et al. 2008; Isbell et al. 2011) como de la diversidad α (Zavaleta et al. 2010) se muestran más significativos a medida que se consideran más funciones simultáneamente, es decir, cuando el foco se pone sobre la multifuncionalidad de los ecosistemas. Por otro lado, la multifuncionalidad depende fuertemente de la escala espacial a la que es evaluada. Diversos estudios empíricos sugieren que se requiere un tamaño mínimo de hábitat para albergar la diversidad necesaria que permita mantener las funciones de los ecosistemas (Thompson y Gonzalez 2016). Las evidencias recogidas hasta la fecha apuntan a que los mayores valores de multifuncionalidad se dan a escalas regionales, especialmente cuando las distintas localidades presentan comunidades que difieren entre sí (Zavaleta et al. 2010; Pasari et al. 2013). Debido a dificultades puramente logísticas, la mayoría de los numerosos estudios empíricos realizados hasta el momento se centran en escalas espaciales pequeñas (ver apartado 3.2.2), y abordan sólo una parte de las funciones de los ecosistemas y los componentes de la biodiversidad. Así, una de las limitaciones más evidentes de estos estudios es

precisamente debida a la existencia de estas relaciones complejas, que requieren una aproximación multifuncional significativamente costosa en términos de tiempo y medios materiales.

Precisamente, en un reciente estudio acerca de las relaciones entre numerosos grupos tróficos y funciones y servicios de los ecosistemas, se detectaron mayores efectos al estudiar la riqueza multi-trófica (Soliveres et al. 2016). Estos resultados apuntan a que la multifuncionalidad de los ecosistemas se explica mejor cuando se tiene en cuenta un mayor número de grupos tróficos y, por tanto, restringir las investigaciones a uno o pocos grupos podría infra-estimar considerablemente la importancia de la biodiversidad en las funciones y el suministro de servicios de los ecosistemas. Esto es coherente con los resultados obtenidos en la revisión sistemática llevada a cabo en el capítulo 2.1 de esta Tesis, donde se observa que los efectos de un mismo impulsor directo de cambio sobre unos u otros grupos de organismos no sólo difieren en relación a los componentes de diversidad funcional analizados, sino que se pueden traducir también en efectos distintos sobre el suministro de servicios de los ecosistemas. Por ello, dado que el rol funcional de cada grupo de organismos es potencialmente distinto en un mismo ecosistema expuesto a los efectos de un determinado impulsor directo de cambio, tanto mejor se podrán conocer sus consecuencias sobre la multifuncionalidad de los ecosistemas cuanta mayor diversidad de organismos se analicen simultáneamente. Si bien este tipo de análisis requieren un considerable esfuerzo y un conocimiento profundo de diferentes grupos de organismos, se postulan como el camino a seguir en las investigaciones que traten de explorar los mecanismos que subyacen a todas estas relaciones complejas en aquellos ecosistemas expuestos a los impulsores directos de cambio.

Por otra parte, los resultados del capítulo 2.2 contribuyen a dar luz a esta cuestión al aportar nuevas pruebas empíricas acerca de los diferentes efectos que cuatro tipos de usos de suelo con distinto grado de intensificación pueden tener sobre la biodiversidad, en función del grupo de organismos estudiado. Si bien los efectos de los diferentes usos de suelo sobre las variables de diversidad taxonómica y funcional fueron marcadamente contexto-dependientes, precisamente dichos resultados son reflejo de la complejidad que subyace a estas relaciones, cuya exploración se convierte en un reto ineludible cuando nuestras preguntas de investigación se dirigen, finalmente, hacia el

mantenimiento de la multifuncionalidad de los ecosistemas en un contexto de Cambio Global.

3.2 Los rasgos funcionales como aproximación para entender los vínculos entre los impulsores directos de cambio y los servicios de los ecosistemas: el Santo Grial de la ecología funcional

La búsqueda de una mayor comprensión de las respuestas de la biodiversidad a los impulsores de cambio, así como de los efectos de la biodiversidad sobre los servicios de los ecosistemas conforma lo que Lavorel y Garnier (2002) han denominado **"el Santo Grial" de la ecología funcional**. El marco basado en rasgos funcionales de "respuesta y efecto" que contextualiza nuestra investigación, está ampliamente reconocido como una herramienta muy útil para incorporar y entender las dinámicas de las comunidades en las predicciones sobre los efectos del Cambio Global (Suding et al. 2008). Concretamente, cada vez más estudios tratan de identificar aquellos rasgos funcionales que puedan actuar simultáneamente como "rasgos de respuesta" y "rasgos de efecto" frente a un determinado impulsor de cambio. Uno de los objetivos perseguidos en el capítulo 2.1 de la presente Tesis fue identificar aquellos rasgos funcionales que actúan como respuesta y/o efecto en los estudios realizados hasta la fecha. Los resultados obtenidos son coherentes con investigaciones previas que han identificado algunos rasgos funcionales que actúan simultáneamente como "respuesta y efecto", tales como el tamaño corporal o aquellos rasgos relacionados con la posición trófica (Schmitz 2004; Larsen et al. 2005). Además, nuestro estudio también permitió identificar otros rasgos "respuesta y efecto", como la actividad de dispersión, el ciclo de vida, o la morfología foliar, entre otros. Más allá de esto, probablemente la contribución más relevante del capítulo 2.1 es que permite poner el foco en el contexto donde se detectan dichos rasgos funcionales "respuesta y efecto", es decir, identificar **(i)** a qué grupo(s) taxonómico(s) pertenecen, **(ii)** ante qué impulsores de cambio responden o **(iii)** sobre qué servicio(s) de los ecosistemas tienen efecto. Como se discute en el propio capítulo, estos resultados pueden estar en parte sesgados por el número de estudios existentes, claramente desbalanceado entre impulsores de cambio, grupos taxonómicos y servicios de los ecosistemas. Sin embargo, pese a las limitaciones que presenta la interpretación de los resultados, podemos destacar algunos patrones y vacíos de información que

deberían ser explorados en el futuro, de cara a lograr una mejor comprensión del marco basado en rasgos funcionales de "respuesta y efecto" (ver Caja 3.1).

Caja 3.1 Vacíos y necesidades de información para avanzar en la investigación basada en el marco de los rasgos funcionales de "respuesta y efecto"

- Ahondar en la identificación de los **rasgos de "respuesta y efecto"** especialmente de los **grupos taxonómicos menos explorados** hasta el momento (como los vertebrados) a través de más estudios enfocados en dichos grupos.
- Explorar en mayor profundidad los **efectos de cada impulsor directo de cambio sobre los rasgos respuesta**. Esto permitiría diseñar estudios y estrategias de conservación y gestión más eficientes en función del impulsor(es) directo(s) de cambio que se encuentre afectando al ecosistema o sistema socio-ecológico objeto de estudio.
- Testar, a través de más casos de estudio, si los rasgos funcionales ya identificados como respuesta y efecto (por ejemplo, tamaño corporal) pueden ser útiles en aquellos ecosistemas menos explorados hasta la fecha. Esta podría ser una de las cuestiones más trascendentes para las investigaciones futuras, ya que la **selección de los rasgos funcionales idóneos para** tratar de **predecir los efectos de los impulsores de cambio** puede convertirse en la herramienta clave que permita el desarrollo de estrategias que palien algunas de las consecuencias más negativas sobre los servicios y funciones de los ecosistemas.
- Explorar si los rasgos funcionales que actúan simultáneamente de respuesta y de efecto presentan **proporcionalidad entre la respuesta al impulsor directo de cambio y sus efectos sobre funciones y servicios de los ecosistemas**. Es decir, se trataría de esclarecer la "importancia" relativa de dichas interacciones para cada rasgo funcional, de forma que pueda identificarse con facilidad si determinados impulsores directos de cambio afectan más intensamente a ciertas funciones y servicios de los ecosistemas, o bien, su efecto sobre alguno de ellos es mínimo. Así, se podría contribuir a diseñar medidas de gestión y conservación de la biodiversidad que minimicen el efecto de los impulsores de cambio sobre aquellos servicios o funciones de los ecosistemas que se consideren prioritarios.

Por otro lado, las relaciones que se establecen entre los rasgos funcionales de las especies y los servicios de los ecosistemas son complejas, ya que por ejemplo un único rasgo funcional puede afectar a varios servicios de los ecosistemas, y a su vez un solo servicio puede verse influido por varios rasgos funcionales (Laureto et al. 2015). Además, se sabe que la pérdida de biodiversidad no es un proceso aleatorio (Dirzo et al.

2014), sino que las especies con determinados valores en algunos rasgos funcionales (mayor masa corporal, tasa lenta de crecimiento, baja tasa de reproducción, etc.) desaparecen a menudo a mayor velocidad (Díaz et al. 2006). Es decir, la pérdida de biodiversidad es más acusada en las especies que presentan determinados rasgos funcionales; y a su vez, esta pérdida neta de algunos rasgos funcionales tiene consecuencias desiguales sobre las funciones y servicios de los ecosistemas. Por ello, para conservar estas funciones y servicios necesitamos conocer aquellos rasgos funcionales más relevantes para su mantenimiento y que, a su vez, se encuentren más amenazados por los procesos de pérdida de biodiversidad. Una vez más, los rasgos funcionales de "respuesta y efecto" se presentan como engranajes determinantes en el avance de la investigación acerca de los efectos del Cambio Global (responsable principal de la pérdida de biodiversidad) sobre los servicios de los ecosistemas.

¿Cómo afrontar la elección de los rasgos funcionales?

Una de las cuestiones más limitantes de la aproximación basada en rasgos funcionales para abordar problemas ecológicos es, precisamente, la elección de dichos rasgos funcionales para cada caso de estudio (Funk et al. 2016). Conocer los rasgos funcionales de los organismos directamente implicados en los mecanismos ecológicos que subyacen a distintos procesos en una comunidad o ecosistema es una tarea altamente compleja. Sin embargo, nos encontramos ante un desafío al que es imperativo enfrentarse, ya que para poder poner el foco en los procesos ecológicos es fundamental entender cómo funcionan dicho(s) procesos(s) y qué organismos y rasgos funcionales se ven más afectados (Petchey y Gaston 2006).

Para abordar las relaciones complejas en el contexto del Cambio Global usando el marco basado en rasgos funcionales de "respuesta y efecto", resulta fundamental identificar los rasgos funcionales con capacidad para suministrar múltiples servicios de los ecosistemas y que, además, respondan a los impulsores directos de cambio. Es por ello que una de las aportaciones más destacadas del capítulo 2.1 de esta Tesis es la identificación de algunos de estos rasgos que fueron denominados "**rasgos funcionales clave**" que actúan, por tanto, como rasgos de respuesta y de efecto simultáneamente. Pero además, debe tratarse de rasgos funcionales **relativamente fáciles de medir** (lo cual permitiría su utilización en todo tipo de casos de estudio, incluso aquellos con

recursos más limitados), y que sean **relevantes en un rango amplio de organismos**. Así, se identificaron algunos de ellos (como el tamaño corporal) que actúan como rasgos de respuesta al cambio de uso del suelo y como rasgos de efecto sobre algunos servicios de los ecosistemas (dispersión de semillas, control de plagas, etc.) para varios grupos de organismos, siendo además fáciles de medir. Sin embargo, es necesario tener en cuenta que existen aún vacíos de información en el estudio de las relaciones entre los impulsores de cambio y el suministro de servicios de los ecosistemas mediados por los rasgos de "respuesta y efecto", especialmente en el caso de los vertebrados. Esto implica que podrían existir otros rasgos funcionales clave que actualmente no parecen relevantes debido a la ausencia o escaso número de estudios que los analizan desde este marco. Es por ello que la identificación de rasgos funcionales clave y su potencial utilidad para el monitoreo de los impactos del Cambio Global sobre los ecosistemas vendrán marcadas por el previsible aumento del número de investigaciones que exploren los vacíos de información existentes en la actualidad.

Por otra parte, las funciones de los ecosistemas así como el suministro de servicios de los ecosistemas, pueden estar mediados por varios rasgos funcionales clave simultáneamente, por lo que identificar estas posibles **agrupaciones** (*bundles*) de rasgos que responden a un determinado impulsor de cambio y explican (aunque sea con distinto grado de intensidad) algunas funciones de los ecosistemas o influyen en el suministro de servicios es otra propuesta planteada también en el capítulo 2.1. La identificación de agrupaciones de rasgos funcionales podría resultar muy útil para diseñar políticas ambientales robustas que permitieran priorizar la conservación de especies que aseguren la presencia de los rasgos funcionales clave (individuales o en agrupaciones) en el ecosistema del que se trate.

En cualquier caso, conviene resaltar que la potencial aplicación del marco basado en rasgos funcionales de "respuesta y efecto" para el diseño de políticas ambientales se plantea aquí no con vocación de reemplazo de otras estrategias actualmente más usadas en las políticas de conservación y manejo del territorio (p.ej., aquellas basadas en la conservación de especies y espacios naturales), sino como una **aproximación complementaria** a las mismas. Debido precisamente a la complejidad que subyace al funcionamiento de los ecosistemas, una aproximación basada en la identificación y conservación de rasgos funcionales clave ha de estar orientada principalmente a la comprensión de los mecanismos ecológicos que determinan las relaciones en el

continuo “Impulsores directos de cambio-Biodiversidad-Servicios de los ecosistemas”, de cara a contribuir (junto a otras aproximaciones) al desarrollo e implementación de mejores estrategias de conservación y gestión de los ecosistemas.

El rol de la redundancia funcional en el marco basado en rasgos funcionales de “respuesta y efecto” y sus relaciones con la resiliencia de los ecosistemas

Las especies funcionalmente redundantes juegan un papel similar en los procesos de los ecosistemas, es decir, la redundancia implica estabilidad funcional ya que la pérdida de especies se compensa con la presencia de otras funcionalmente similares (“**Hipótesis de la redundancia funcional**”, Naeem et al. 2009). Cuando varias especies difieren en sus respuestas a los impulsores de cambio que ejercen como perturbaciones (diversidad de respuesta), aumentan las opciones de que al menos algunas de dichas especies persistan al cambio y continúen contribuyendo al suministro de servicios de los ecosistemas (Elmqvist et al. 2003). La resiliencia de un ecosistema para suministrar un determinado servicio puede estar comprometida por la presencia de una o varias especies clave para el suministro de dicho servicio que presenten valores bajos de redundancia funcional (incluso cuando los valores generales de redundancia del ecosistema sean altos) (Kotschy 2013). Sin embargo, el papel de la redundancia funcional de una comunidad en la generación y/o mantenimiento de las funciones y servicios de los ecosistemas es una cuestión aún controvertida en la comunidad científica (Mori et al. 2013).

Como se menciona en la sección de Introducción, las principales preguntas de investigación planteadas en esta Tesis se enmarcan en las Ciencias de la Sostenibilidad, y éstas a su vez están profundamente ligadas al concepto de **resiliencia** de los ecosistemas. Aunque existen múltiples aproximaciones a este concepto, en el presente trabajo se entiende la resiliencia ecológica como “la capacidad de un ecosistema para absorber perturbaciones y reorganizarse mientras está experimentando o tras experimentar cambios, de forma que pueda mantener básicamente la misma estructura, funcionamiento y mecanismos de auto-regulación” (Walker et al. 2004). Desde este marco conceptual se asume que los cambios forman parte de las dinámicas naturales de cualquier ecosistema o sistema socio-ecológico, pudiendo éstos tener respuestas más o menos efectivas ante dichos cambios o perturbaciones (Folke et al. 2003).

Los resultados del capítulo 2.1 de esta Tesis han permitido identificar algunos patrones de relaciones y vacíos de información que abren el camino a futuras investigaciones que permitirían dibujar estrategias de priorización en la gestión de los ecosistemas para mantener su resiliencia en un contexto de Cambio Global. De hecho, la identificación de los rasgos funcionales clave podría tener implicaciones trascendentales sobre la **capacidad adaptativa** de los ecosistemas en el contexto del Cambio Global (Nimmo et al. 2015; Seidl et al. 2015) aportando ciertas garantías para el mantenimiento del suministro de los servicios de los ecosistemas en sí mismos (Díaz et al. 2013; Biggs et al. 2012, 2015).

Por otra parte, los resultados del estudio empírico realizado para el capítulo 2.2 muestran que en las dehesas (uno de los usos del suelo del caso de estudio, con un grado de intensificación bajo) los valores de diversidad taxonómica de aves y vegetación herbácea fueron significativamente superiores a los registrados en los otros usos del suelo estudiados, mientras que los valores de diversidad funcional se mantuvieron en valores intermedios. Es decir, en las dehesas se encontró un mayor número de especies de aves y herbáceas, muchas de cuales desempeñan un papel funcional similar. Estos resultados sugieren que los usos del suelo con **formas de manejo extensivas**, como las dehesas, pueden **albergar una mayor redundancia funcional** en algunos grupos de organismos, lo que puede traducirse en una **mayor resiliencia** frente a los posibles impulsores de cambio. Desde una perspectiva multidimensional, las dehesas se encuentran entre los agroecosistemas mediterráneos con mayor valor ecológico y cultural (Gómez Sal y González García 2007), al combinar funciones productivas y no productivas como resultado de un modelo tradicional de uso del territorio muy resiliente y con alta coherencia ecológica (Gómez Sal et al. 2003).

<u>Potencial de los rasgos funcionales para desarrollar reglas predictivas generales en las comunidades biológicas</u>

Son muchos los factores que pueden influir en la compleja estructura de un determinado ecosistema. Afrontar el estudio de todos ellos se plantea como un objetivo inabordable debido al ingente número de mediciones que habría que llevar a cabo para lograrlo. Es por ello que la priorización del estudio de los factores que tienen un papel relevante en

la estructura y funcionamiento de los ecosistemas se ha convertido en uno de los retos más interesantes en la Ecología de los últimos años (McGill et al. 2006).

Diversas investigaciones han demostrado que los rasgos funcionales explican en gran medida la estructura y función de las comunidades biológicas (Sutton-Grier y Megonigal 2011; de Bello et al. 2012; Edwards et al. 2013). Los resultados que muestran la influencia de los rasgos funcionales en la estructura de las comunidades conducen a valorar la posibilidad de desarrollar reglas predictivas generales a medida que se siga avanzando en la comprensión del rol de los diferentes rasgos "respuesta y efecto" (Funk et al. 2016).

El uso de los rasgos funcionales tiene también un gran potencial en la evaluación de las políticas de gestión de los servicios de los ecosistemas, debido a su naturaleza como variable continua y las relaciones directas detectadas con diversos procesos ecológicos (Westoby y Wright 2006). Así, la posibilidad de realizar mediciones cuantitativas y cualitativas de rasgos funcionales en relación a otros factores que nos interese explorar contribuye a la identificación de patrones generales que, finalmente, pueden derivar en el desarrollo de reglas predictivas. Además, en los últimos años se han venido desarrollando e implementando nuevas herramientas metodológicas (especialmente en relación con los análisis estadísticos) que permiten medir nuevas facetas de la diversidad funcional en las comunidades (Mouchet et al. 2010). Aún son pocos los estudios que han utilizado los rasgos funcionales para cuantificar las diferencias en las comunidades tras haberse producido un cambio ambiental (Cadotte et al. 2015). Sin embargo, recientemente se ha creado un nuevo marco conceptual basado en el uso de los rasgos funcionales como herramienta para realizar predicciones de la abundancia de especies en las comunidades biológicas (Laughlin et al. 2012; Laughlin 2014). Así, este paso adelante en el uso de los rasgos funcionales abre la primera puerta en el avance de la ecología funcional para abordar lo que hasta el día de hoy es todavía un reto: desarrollar reglas predictivas generales en las comunidades biológicas basadas en el uso de los rasgos funcionales.

3.3 Retos futuros para la investigación basada en el marco de los rasgos funcionales de "respuesta y efecto": desafíos metodológicos y nuevas fronteras

A pesar del aumento constante de las investigaciones que exploran los vínculos en el continuo “Impulsores directos de cambio-Biodiversidad-Servicios de los ecosistemas”, se trata de una línea de investigación muy joven en la que falta aún mucho conocimiento científico. De los resultados obtenidos tras estos primeros años de investigación emanan una larga lista de cuestiones que necesitan ser exploradas en mayor profundidad en futuros estudios. La Tabla 3.1 sintetiza algunas de las principales cuestiones clave en relación a las limitaciones metodológicas existentes hasta la fecha, algunas propuestas sobre nuevos usos de los rasgos funcionales, y desafíos futuros para mejorar el conocimiento actual de las relaciones complejas estudiadas desde el marco basado en rasgos funcionales de “respuesta y efecto”.

Retos futuros	Cuestiones clave	¿Por qué es importante?
Valorar la diversidad intraespecífica en los rasgos funcionales	¿Cómo desarrollar protocolos estandarizados de medición y valoración de rasgos funcionales que permitan abordar la variabilidad intraespecífica de los mismos? ¿Cómo gestionar listas estandarizadas de rasgos funcionales relevantes para el estudio de los vínculos entre impulsores directos de cambio y servicios de los ecosistemas en distintos contextos geográficos?	Se ha demostrado que la diversidad intraespecífica de los rasgos funcionales puede afectar a las dinámicas ecológicas y las funciones de los ecosistemas. Por ello, la medición de los rasgos funcionales de los organismos en cada caso de estudio podría aportar una información mucho más precisa de su respuesta real frente a un determinado cambio (y por tanto, también acerca de su rol en las funciones y servicios de los ecosistemas).
Ampliar las escalas espacio-temporales de los estudios basados en rasgos funcionales	¿Cómo diseñar programas de investigación y monitoreo a medio y largo plazo sobre el efecto de los impulsores de cambio en los servicios de los ecosistemas, a través de rasgos funcionales? ¿Cómo diseñar estudios empíricos basados en rasgos funcionales de respuesta y efecto que, más allá de lo local, aborden también las escalas regionales y globales?	Ampliar las escalas de análisis más allá de lo local y asegurar el monitoreo a largo plazo de los rasgos funcionales resulta fundamental para poder comprender y predecir mejor los efectos de los impulsores de cambio sobre la biodiversidad, así como para la potencial aplicación del marco de rasgos funcionales de respuesta y efecto en las políticas ambientales y la gestión de los ecosistemas.
Aplicar enfoques multitróficos	¿Cómo son las interacciones entre rasgos funcionales de distintos grupos de organismos pertenecientes a varios niveles tróficos? ¿Cómo pueden afectar dichas interacciones a las funciones y servicios de los ecosistemas? ¿Cómo promover la investigación basada en rasgos funcionales en aquellos grupos taxonómicos menos estudiados?	Dadas las respuestas tan diferentes mostradas por distintos tipos de organismos frente a los impulsores de cambio, profundizar en los enfoques multitróficos de la investigación resulta fundamental de cara a una comprensión global del efecto de los impulsores y sus vínculos con las funciones y servicios de los ecosistemas.
Explorar el papel de la rareza en la multifuncionalidad	¿Qué papel desempeñan los rasgos funcionales de las especies raras en la respuesta a los impulsores de cambio y en la generación de servicios? ¿Puede el estudio de los	Dado que las especies raras pueden ser elementos clave que aumentan la diversidad funcional de las comunidades, priorizar los esfuerzos en identificar el papel de los rasgos funcionales de las

de los ecosistemas y la generación de servicios	rasgos funcionales de las especies menos abundantes contribuir a una mejor comprensión de las relaciones entre impulsores de cambio y servicios de los ecosistemas?	especies menos abundantes implicaría un salto cualitativo para comprender la vulnerabilidad real de las funciones y servicios de los ecosistemas frente a los impulsores de cambio.
Identificar, caracterizar y cartografiar las Unidades Proveedoras de Multifuncionalidad	¿Es posible caracterizar Unidades Proveedoras de Multifuncionalidad que contribuyan a desarrollar estrategias de gestión que garanticen su mantenimiento? ¿Cómo plasmar las Unidades Proveedoras de Multifuncionales en la cartografía del territorio?	Caracterizar y cartografiar Unidades Proveedoras de Multifuncionalidad resulta fundamental para una planificación del territorio orientada al mantenimiento de la capacidad de los ecosistemas de suministrar múltiples funciones y servicios en un contexto de Cambio Global.

Tabla 3.1. Preguntas clave para abordar los desafíos metodológicos y los retos futuros de la investigación basada en rasgos funcionales de "respuesta y efecto".

La obtención de valores para los rasgos funcionales: clave para explorar el continuo "Impulsores directos de cambio-Biodiversidad-Servicios de los ecosistemas"

La obtención de los valores de los rasgos funcionales supuso uno de los primeros retos de los estudios empíricos de esta Tesis. Por un lado, respecto a los **rasgos funcionales cualitativos** (como por ejemplo el tipo de dieta, método de dispersión, forma de crecimiento, etc.), se optó por búsquedas bibliográficas y consultas a colaboradores/as con demostrada experiencia. Sin embargo, la principal limitación radica en la obtención de los **rasgos funcionales cuantitativos**, para la cual existen principalmente dos aproximaciones: (i) la consulta en bases de datos disponibles en la bibliografía o a través de distintas plataformas *online* (como Try-database, LEDA, GLOPNET, entre otras); o bien (ii) la medición de los rasgos funcionales en el campo o en muestras en laboratorio, con la consiguiente inversión adicional de tiempo y materiales.

Estas dos aproximaciones para obtener los rasgos funcionales cuantitativos ponen sobre la mesa un debate acerca de las limitaciones e idoneidad de cada una de ellas. Por un lado, el uso de bases de datos provenientes de trabajos previos permite acceder a información de rasgos funcionales cuya recolección *in situ* implicaría un trabajo de campo y laboratorio muy elevado (Moretti y Legg 2009) y, en ocasiones, la utilización de técnicas costosas (Cornelissen et al. 2003). En contraposición, la medición de los rasgos funcionales en cada caso de estudio permite obtener unos datos que reflejan de manera precisa la realidad concreta de la zona, pero en muchas ocasiones implica un gran esfuerzo de muestreo. En los capítulos 2.2 y 2.3 se utilizaron ambas aproximaciones simultáneamente para obtener los rasgos funcionales seleccionados para cada grupo taxonómico en los casos de estudio. De hecho, ésta es probablemente la fórmula más utilizada en las investigaciones ecológicas empíricas cuando se utilizan rasgos funcionales cuantitativos y cualitativos.

Si bien el uso de ambas aproximaciones indistintamente como fuente para la obtención de datos es relativamente habitual, parece necesario plantear algunas cuestiones que podrían generar un interesante debate relacionado con la variación interespecífica e intraespecífica de los rasgos funcionales. La variación intraespecífica de rasgos es reconocida desde hace décadas, y ha sido incorporada en diversos trabajos clásicos de ecología genética y evolución de nicho (Roughgarden 1972; Ford 1977). Sin embargo, desde mediados de los años 70, buena parte de los estudios ecológicos (tanto empíricos como teóricos) han considerado implícitamente que todos los individuos de una misma

especie son intercambiables, es decir, que las características fenotípicas (entre las que se encuentran algunos rasgos funcionales comúnmente utilizados) no son significativamente diferentes entre los individuos de una misma especie.

En los últimos años, algunas investigaciones han puesto de manifiesto que la diversidad intraespecífica de los rasgos funcionales no es irrelevante (de Bello et al. 2013), y de hecho, puede afectar a las dinámicas ecológicas y las funciones de los ecosistemas (Crutzinger et al. 2006; Lecerf y Chauvet 2008; Bolnick et al. 2011). Es por ello que la medición de los rasgos funcionales de los organismos en cada caso de estudio podría aportar una información mucho más precisa de su respuesta real frente a un determinado cambio (y por tanto, también acerca de su rol en la función de los ecosistemas). Además, contar con esta información base permitiría explorar la variabilidad intraespecífica de los rasgos funcionales en función del factor estudiado, lo que haría posible dar un paso más en la comprensión de las relaciones de la diversidad funcional con los impulsores de cambio (a través de los rasgos de respuesta), y con los servicios y funciones de los ecosistemas (a través de los rasgos de efecto).

El papel de las escalas espaciales y temporales en el diagnóstico de los efectos del Cambio Global

Las investigaciones sobre vínculos entre biodiversidad y servicios de los ecosistemas, y las centradas en las relaciones entre biodiversidad y funcionamiento de los ecosistemas avanzan generalmente de forma independiente y con escalas de trabajo diferentes (Duncan et al. 2015). Las escalas temporales y espaciales tienen un papel fundamental en los efectos del Cambio Global sobre la biodiversidad y sus consecuencias sobre las funciones y servicios de los ecosistemas, y por ello deben ser tenidas en cuenta en el diseño de investigaciones futuras. En este sentido, Sternberg y Yakir (2015) destacaron tres de las cuestiones más relevantes para desarrollar dichas investigaciones:

- Es necesario un **enfoque a largo plazo** de las investigaciones que traten de explorar los efectos ecológicos y fisiológicos a nivel de la comunidad, de cara a visibilizar aquellos procesos cuyos ritmos son relativamente lentos.
- Las investigaciones relativas al Cambio Global deben **incorporar** a la investigación observacional y experimental **otros métodos** basados en sistemas

de **modelización y monitoreo**. Esto permitiría obtener unos resultados que tengan en cuenta escalas espaciales y temporales suficientemente grandes y complejas para evaluar los efectos del Cambio Global sobre las funciones de los ecosistemas de una manera más efectiva (Osmond et al. 2004).

- Es preciso discutir de forma integradora en los **marcos nacionales e internacionales** de investigación orientados al Cambio Global, los requisitos necesarios para **abordar** los **estudios a gran escala** (p.ej., necesidad de grandes instalaciones, promover redes de centros de investigación, desarrollar herramientas para abordar grandes escalas de observación, etc.) (Baldocchi et al. 2001; González-Meler et al. 2014).

Sin embargo, las funciones y servicios de los ecosistemas suelen explorarse a pequeña escala espacial en los estudios empíricos (Kremen et al. 2005), en buena medida debido al necesario equilibrio entre la consecución de los objetivos planteados y la inversión de un esfuerzo muestral razonable. Este hecho supone una limitación importante, ya que las escalas que la sociedad suele manejar en relación a dichas funciones y servicios de los ecosistemas son mayores (Pasari et al. 2013) (Fig 3.1). En este sentido, en uno de los casos de estudio desarrollados en la presente Tesis (capítulo 2.2) se exploran precisamente los distintos efectos de cuatro tipos de uso de suelo sobre la diversidad de cuatro grupos de organismos a **dos escalas espaciales diferentes** (diversidad entre unidades muestrales y diversidad entre sitios). Los resultados apuntaron a que tanto la diversidad taxonómica como funcional de los cuatro grupos de organismos estudiados (vegetación herbácea, vegetación leñosa, hormigas y aves) responden de manera diferente a los usos de suelo en función de la escala. Si bien no se pudo describir un patrón concluyente al respecto, sí encontramos que la mayor variabilidad en la diversidad taxonómica fue detectada a escalas mayores, frente a los valores de diversidad funcional, cuya variabilidad fue superior a las escalas espaciales más pequeñas. Estos resultados sugieren que, más allá de que los cambios de uso del suelo pueden producir cambios sobre la biodiversidad a múltiples escalas (Kleijn et al. 2009), existe una necesidad de definir mejor dichos efectos a través de las distintas escalas espaciales, lo cual permitiría **i)** comprender y predecir mejor los efectos de los impulsores de cambio sobre la biodiversidad, y **ii)** diseñar estrategias de manejo a través

de estudios empíricos más eficientes, ajustando los diseños muestrales a los objetivos concretos de cada investigación.

Cuando el objetivo es plantear propuestas de gestión relacionadas con el suministro de determinados servicios de los ecosistemas, es necesario ampliar la obtención de los datos desde la escala local a la escala regional (Abelleira-Martínez et al. 2016). En este sentido, existe un **desacoplamiento** importante en el uso de las **escalas espacio-temporales entre los estudios** centrados en la medición de rasgos funcionales y aquellos que analizan y evalúan el suministro de servicios de los ecosistemas. Bien es cierto que a pequeñas escalas (espaciales y temporales) sí existe un acoplamiento en las mediciones llevadas a cabo en los estudios (la mayor parte de los estudios empíricos que miden rasgos funcionales lo hacen a pequeñas escalas; y los estudios orientados a evaluar o medir servicios de los ecosistemas abordan también estas pequeñas escalas). Sin embargo, a escalas mayores (tanto escalas temporales que impliquen un monitoreo a medio y largo plazo o bien la réplica de muestreos en dos o más años; así como el uso de escalas espaciales regionales, nacionales o globales) sí existe tal desacoplamiento, ya que a estas escalas grandes los estudios que utilizan los rasgos funcionales como herramienta para el análisis de distintas variables son muy escasos, mientras que los estudios que exploran y evalúan el suministro de servicios de los ecosistemas son más numerosos. Es por ello que el uso del marco basado en rasgos funcionales de "respuesta y efecto" como aproximación para explorar los vínculos entre el cambio de uso del suelo y los servicios de los ecosistemas requiere abordar estos vacíos de información que nacen del desacoplamiento existente entre los conocimientos empíricos de los rasgos funcionales y el análisis del suministro de los servicios de los ecosistemas.

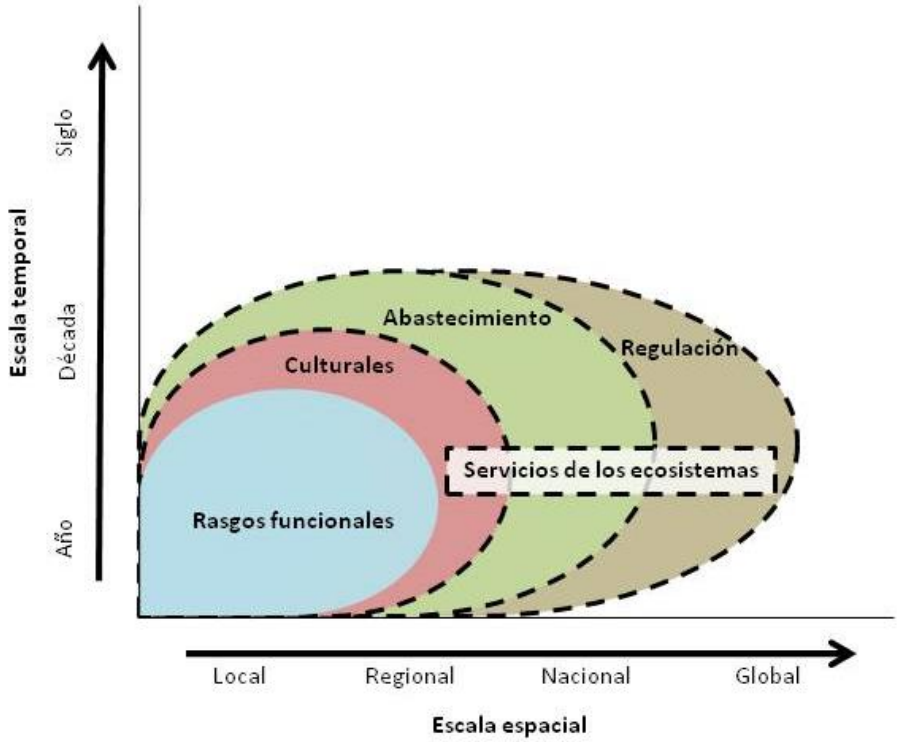

Fig. 3.1 Esquema general del desacoplamiento entre las escalas espacio-temporales a las que se desarrollan más frecuentemente los estudios empíricos que miden y/o evalúan los servicios de los ecosistemas y los que miden rasgos funcionales.

Como se comentó anteriormente, el esfuerzo requerido para la toma de datos de rasgos funcionales determina en buena medida la elección de escalas de trabajo espacio-temporales pequeñas. Sin embargo, resulta imperativo plantear el desarrollo de algunas medidas encaminadas a completar la información referente a otras escalas en futuras investigaciones, tales como aplicar métodos de detección remota, desarrollar diseños muestrales coordinados entre distintos estudios científicos a una escala espacial regional, realizar monitoreos a medio y largo plazo, así como diseñar los muestreos de valoración y medición de servicios de los ecosistemas de forma coordinada con las mediciones de rasgos funcionales.

En este sentido, parece lógico recopilar información a escalas mayores a través de bases de datos de rasgos funcionales de las especies dominantes. Sin embargo, estos métodos de recolección de datos carecen de información clave acerca de los efectos de la variación intraespecífica de rasgos funcionales sobre las funciones de los ecosistemas (Hillebrand et al. 2008), que sin embargo los métodos de obtención de datos *in situ* pueden capturar más apropiadamente (Albert et al. 2011).

La dependencia de los grupos taxonómicos

Los mecanismos ecológicos responsables de las relaciones complejas que detectamos entre la biodiversidad y los servicios de los ecosistemas son alimentados, en mayor o menor medida, por todo el conjunto de organismos presentes en el(los) ecosistema(s) donde se generan (de Bello et al. 2010; Lavorel et al. 2011). En concreto, el efecto de los impulsores directos de cambio sobre los organismos parece claramente dependiente del grupo taxonómico estudiado. Es decir, no se ha descrito hasta la fecha ningún único patrón claro que refleje las respuestas de distintos grupos a un determinado impulsor de cambio, ni siquiera en aquellos estudios que abordan simultáneamente varios grupos (Flynn et al. 2008). De hecho, varios estudios que abordaron las relaciones entre los usos del suelo y diversos grupos taxonómicos arrojaron resultados contradictorios en relación a la intensidad y dirección de dichas relaciones (Wolters et al. 2006; Lewandowski et al. 2010).

Como muestran los resultados del capítulo 2.1, la mayor parte de los estudios realizados hasta la fecha que utilizan el marco basado en rasgos funcionales de "respuesta y efecto", se han centrado en explorar las respuestas de algunos organismos vegetales e invertebrados, y en muy pocos casos de manera conjunta en un mismo estudio. Dadas las respuestas tan distintas de cada grupo de organismos, para una comprensión global del efecto de los impulsores de cambio es necesario ampliar el rango de grupos taxonómicos estudiados. Precisamente, el capítulo 2.2 de la presente Tesis se diseñó con la intención de identificar los patrones de respuesta de varios grupos de organismos (vegetación herbácea y leñosa, hormigas y aves) a cuatro tipos de uso del suelo con distinto grado de intensificación. Los resultados mostraron que, en efecto, las tendencias y respuestas de los valores de diversidad taxonómica y funcional fueron muy diferentes en cada grupo.

A pesar de ello, la respuesta de dichos grupos a los diferentes usos del suelo aporta información necesaria para detectar posibles patrones que pueden ser útiles para comprender mejor el efecto que puede ejercer el cambio de uso del suelo sobre los organismos. Así, el hecho de que el efecto del uso del suelo sobre la diversidad taxonómica y funcional de las comunidades de hormigas fuera identificado únicamente a las escalas más pequeñas (escala de unidad muestral) puede deberse a que son

organismos considerados semi-sésiles, ya que su rango de actividad no suele ser superior a unos pocos metros alrededor del nido (Andersen 1991). En este sentido, los cambios en las comunidades de hormigas están fuertemente determinados por las características del entorno a pequeñas escalas espaciales. Por su parte, la respuesta de organismos muy móviles como las aves, a pesar de no presentar patrones claros de cambio en los valores de diversidad funcional, mostraron valores de diversidad taxonómica significativamente distintos entre los usos del suelo en las dos escalas espaciales utilizadas en este trabajo, es decir, entre unidades muestrales y entre sitios. Como se discute en el propio capítulo 2.2, los resultados apuntan a la necesidad de utilizar escalas espaciales mayores (regionales o globales) suficientes para detectar de manera más evidente potenciales diferencias en valores de diversidad taxonómica y funcional para este grupo en relación a los usos del suelo.

En definitiva, parece que aún quedan algunos pasos por dar para definir las escalas más apropiadas en aquellos estudios que traten de explorar los efectos de los cambios de uso del suelo sobre la biodiversidad en función del tipo o tipos de organismos que se consideren.

El papel de los rasgos funcionales de las especies raras en la funcionalidad de los ecosistemas

Las especies raras han recibido mucha atención desde la biología de la conservación, debido a que su contribución a la extinción global tiene un peso proporcionalmente muy relevante respecto a las especies más abundantes (Van Claster et al. 2008). Sin embargo, los estudios enfocados en analizar distintas variables de la diversidad funcional no suelen tener en cuenta las especies raras ya que los índices son más dependientes de las especies abundantes. Esto se debe a que las especies raras se detectan peor en los muestreos de campo, y en muchos casos tampoco aparecen en las bases de datos internacionales de rasgos funcionales. Esto supone un importante limitante en la comprensión de la mayor parte de los procesos ecológicos clave (como pueden ser la degradación de materia orgánica, la productividad, etc.) que se encuentran amenazados por la pérdida de ciertas funciones llevadas a cabo por especies concretas (Solan et al. 2004; Hector y Bagchi 2007), algunas de las cuales pueden ser además especies raras (Mouillot et al. 2013).

Por otra parte, las combinaciones únicas de rasgos funcionales suelen darse en las especies raras, es decir, en aquellas menos abundantes en un determinado ecosistema (incluso en ecosistemas muy diversos) (Mouillot et al. 2013). De este modo, el papel de la redundancia funcional de un determinado ecosistema puede no ser suficiente para evitar la pérdida de algunos de los procesos ecológicos llevados a cabo por las especies raras (Salgado-Negret 2015). Es por ello que la **medición de rasgos funcionales en las especies menos abundantes** se presenta como un reto futuro de gran relevancia para comprender la vulnerabilidad real de las funciones y servicios de los ecosistemas frente a los impulsores de cambio.

De hecho, la pérdida de especies raras no sólo afecta a los procesos de los ecosistemas a escala local en el corto plazo (Bracken y Low 2012), sino también a escalas espaciales y temporales superiores (Lyons et al. 2005). A pesar de que existen ciertas controversias, en diversas investigaciones previas se ha identificado a las especies raras como elementos clave que aumentan la diversidad funcional de las comunidades locales (Richardson et al. 2012) ya que proporcionan determinados rasgos funcionales que, aunque escasos en la comunidad, intervienen en muchas de las principales funciones de los ecosistemas (Mouillot et al. 2011). Por tanto, seguir explorando esta línea de investigación a través de casos de estudio puede resultar crucial en el avance de la ecología funcional. Priorizar los esfuerzos en identificar las especies raras de los ecosistemas objeto de estudio para entender mejor el funcionamiento de los ecosistemas, y por tanto, evaluar mejor los efectos funcionales de un determinado impulsor de cambio implicaría un salto cualitativo en la comprensión de las relaciones complejas que subyacen a las funciones y al suministro de servicios de los ecosistemas.

La identificación de “unidades proveedoras de multifuncionalidad”

Existen dos formas clásicas de entender el concepto de “unidades proveedoras de servicios (UPS)”. Algunos autores las definen como aquellos lugares físicos que proporcionan, o pueden proporcionar en el futuro, uno o varios servicios de los ecosistemas en alguna escala temporal o espacial (Luck et al. 2003; García-Nieto et al. 2013). Por otro lado, las UPS se pueden definir mediante la relación entre organismos y servicios de los ecosistemas. En este sentido, Kremen et al. (2005) denominó “suministradores de servicios” a aquellos organismos que realizan funciones que pueden traducirse en servicios de los ecosistemas en diferentes escalas ecológicas (especies,

comunidades, etc.). La fusión de ambas aproximaciones desemboca en un concepto de UPS más integrador, entendido como unidades espacialmente explícitas, dependientes del contexto (en el que se incluye la presencia de organismos), y generadoras de servicios de los ecosistemas (Andersson et al. 2015).

Desde hace algunos años, se está profundizando en el conocimiento acerca de las características clave de las UPS (como la biodiversidad estructural o la composición del hábitat) que pueden afectar de manera más determinante a la provisión de servicios de los ecosistemas (Maes et al. 2012; Luck 2016). Abordar este nuevo reto permitiría dar un salto cualitativo en las investigaciones que exploran las UPS, de modo que se aborden considerando grupos funcionales de múltiples especies, comunidades ecológicas completas, tipos de hábitats, etc.

Así, depositar mayores esfuerzos en la identificación de componentes de la biodiversidad (por ejemplo los grupos tróficos, o los rasgos funcionales) que influyen en la provisión de servicios y funciones de los ecosistemas podría permitir también la delimitación de **unidades proveedoras de multifuncionalidad (UPM)**. Más aún, sería posible definir "UPM clave", entendidas como aquellas unidades espacialmente explícitas con altos valores de redundancia funcional y agrupaciones (*bundles*) de rasgos funcionales que responden a los efectos del Cambio Global y tienen a su vez efectos sobre la multifuncionalidad de los ecosistemas.

Ciertamente la inclusión de la delimitación espacial en las definiciones de las UPSs y las UPMs entraña muchas complicaciones, especialmente en relación a la dificultad de delimitar en el espacio una unidad compuesta principalmente por tipos de relaciones complejas, en las que habitualmente no se conocen ni siquiera todos los componentes biofísicos que las conforman. Sin embargo, comprender la variabilidad existente en el territorio desde el punto de vista de su potencialidad para la generación de funciones y servicios de los ecosistemas, y poder plasmar esta variabilidad de forma tangible en el espacio, resultaría crucial para desarrollar propuestas encaminadas a la toma de decisiones ecológica y económicamente sostenibles (Kremen 2005).

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Capítulo 4

Conclusiones

Conclusiones

- Se han encontrado múltiples evidencias de los vínculos entre impulsores directos de cambio y servicios de los ecosistemas, mediados por rasgos funcionales. La mayor parte de estas evidencias hacen referencia al efecto de los cambios de uso del suelo sobre varios servicios de regulación, principalmente a través de rasgos funcionales de plantas e invertebrados. Sin embargo, existen aún importantes vacíos de información y sesgos en las investigaciones basadas en el marco de rasgos funcionales de "respuesta y efecto", especialmente en cuanto al tipo de ecosistemas, grupos taxonómicos, e impulsores directos de cambio estudiados, así como respecto al rango geográfico y las escalas espaciales analizadas.

- Las evidencias empíricas sugieren la existencia de muchos rasgos que tienen la capacidad de responder a los impulsores directos de cambio (rasgos funcionales de respuesta), influyendo también en el suministro de múltiples servicios de los ecosistemas (rasgos funcionales de efecto). Algunos de estos rasgos que actúan simultáneamente como respuesta y efecto resultan, además, relativamente fáciles de medir y son relevantes en un rango amplio de organismos, lo cual los convierte en "rasgos funcionales clave", con potenciales aplicaciones para el monitoreo de los efectos del Cambio Global sobre los ecosistemas.

- Las transformaciones vinculadas a la intensificación del uso del suelo tienen importantes efectos sobre la diversidad taxonómica y funcional. Sin embargo, estos efectos son altamente contexto-dependientes, variando en función del tipo de organismo estudiado y la escala espacial de análisis. Futuras investigaciones sobre el efecto de los cambios de uso del suelo deberían tener en cuenta las particularidades de cada sitio de estudio, así como el efecto de la escala espacial y el grupo biótico, a la hora de analizar las posibles trayectorias de cambio en los valores de diversidad taxonómica y funcional.

- En el contexto de los agroecosistemas mediterráneos, usos del suelo con formas de manejo extensivo, como el caso de las dehesas, presentan altos valores de redundancia funcional (es decir, albergan numerosas especies con rasgos

funcionales similares). Este hecho se puede traducir en una mayor resiliencia de dichos agroecosistemas frente a los posibles efectos de los impulsores directos de cambio.

- Las vías pecuarias con uso ganadero actúan como reservorios de poblaciones de hormigas funcionalmente diversas, y tienen también un efecto positivo sobre la diversidad de hormigas en los cultivos intensivos adyacentes. Además, ejercen un papel importante como reservorio de poblaciones de abejas silvestres, especialmente relevante en paisajes de agricultura intensiva como los dominados por cultivos de girasol. El mantenimiento de una red de vías pecuarias activas es altamente dependiente de su uso por parte del ganado trashumante, por lo que salvaguardar la sostenibilidad socio-económica de esta práctica tradicional constituye un desafío fundamental para contribuir al mantenimiento de agroecosistemas multifuncionales con capacidad adaptativa ante los efectos de los impulsores directos de cambio.

- Las visitas de las abejas silvestres a los girasoles aumentan cerca de una vía pecuaria, resultando en una mayor producción de semillas en las áreas adyacentes a la misma, incluso en condiciones de alta abundancia de abejas melíferas. Para garantizar una efectiva polinización en cultivos como el girasol, altamente dependientes de los insectos polinizadores, será necesario priorizar en las futuras políticas agrícolas la conservación de hábitats naturales y/o semi-naturales (como las vías pecuarias), especialmente en paisajes de agricultura intensiva.

- El marco de investigación basado en rasgos funcionales de "respuesta y efecto" se ha mostrado muy útil para mejorar la comprensión de las relaciones complejas existentes entre los impulsores directos de cambio y las funciones y servicios de los ecosistemas. Sin embargo, se han identificado una serie de cuestiones prioritarias que deberían ser exploradas en futuras investigaciones en aras de potenciar la aplicabilidad de este marco en las políticas ambientales. Entre los retos futuros de investigación destacan: i) explorar la variabilidad intraespecífica en los rasgos funcionales y crear protocolos de medición y listas estandarizadas de dichos rasgos; ii) ampliar las escalas espacio-temporales de los

estudios empíricos y diseñar programas de investigación y monitoreo a medio y largo plazo; iii) aplicar enfoques multitróficos y promover la investigación basada en rasgos funcionales de los grupos de organismos menos estudiados; iv) explorar el papel desempeñado por los rasgos funcionales de las especies menos abundantes en la multifuncionalidad de los ecosistemas y el suministro de servicios; v) identificar, caracterizar y cartografiar "unidades proveedoras de multifuncionalidad", entendidas como aquellas unidades espacialmente explícitas con altos valores de redundancia funcional y agrupaciones de rasgos funcionales que responden a los efectos del Cambio Global y tienen a su vez efectos sobre la multifuncionalidad de los ecosistemas.

Conclusions

- Much evidence exists on the links between the direct drivers of change and ecosystem services mediated by functional traits. Most of this evidence focuses on how land use change affects several regulating services, through functional traits of vegetation and invertebrates. However, there remain important information gaps and biases in studies based on the framework of "response and effect" functional traits, especially regarding the type of ecosystems, taxonomic groups, direct drivers of change, geographic range, and spatial scale analyzed.

- Empirical evidence suggests that there are many traits that have the capacity to respond to specific direct drivers of change (response traits), and also influence the provision of multiple ecosystem services (effect traits). Some of these traits may be considered as "key functional traits", being defined as those that act simultaneously as response and effect, and are also relatively easy to measure and relevant for a wide range of organisms. These attributes make them particularly useful for monitoring the effects of Global Change on ecosystems.

- Land use changes associated with intensification have important effects on taxonomic and functional diversity. However, these effects are highly context-dependent, and vary depending on the biotic group being studied and the spatial scale of the analysis. Future research on the effects of land use change should take into account the particularities of each study site, as well as the effect of the spatial scale and the biotic group, when analyzing all possible trajectories of change in relation to the values of taxonomic and functional diversity.

- In the context of Mediterranean agroecosystems, land uses subject to extensive management practices (such as *dehesas*) exhibit high values of functional redundancy (i.e., they host numerous species sharing similar functional traits). This fact might increase the resilience of these agroecosystems when exposed to the possible effects of direct drivers of change.

- Livestock drove roads act as reservoirs of ant communities with high functional diversity, and have a positive effect on ant diversity in adjacent intensive

cropping systems. Furthermore, drove roads are important reservoirs of wild bee populations, which is particularly relevant within intensive agricultural landscapes, such as those dominated by sunflower crops. The maintenance of an active network of drove roads is largely dependent on their use by transhumant livestock. Thus, safeguarding the socio-economic sustainability of this traditional practice constitutes a fundamental challenge for maintaining multifunctional agroecosystems, with adaptive capacity to cope with the effects of direct drivers of change.

- Wild bee visitation to sunflowers is higher closer to the drove road, resulting in increased seed production in adjacent areas, even when the abundance of honey bees is high. To ensure the effective pollination of sunflower crops (highly dependent on insect pollinators), it is necessary for future agricultural policies to prioritize the conservation of natural and/or semi-natural habitats (such as drove roads), especially in intensive agricultural landscapes.

- The research framework based on the "response and effect" functional traits proved very useful to improve our understanding of the existing complex relationships between the direct drivers of change and ecosystem functions and services. However, we identified several priority questions that should be explored by future studies to enhance the applicability of this framework in environmental policies. Future research challenges include: i) exploring the intraspecific variability of functional traits, and creating measurement protocols and standardized lists of such traits; ii) expanding the spatio-temporal scales of empirical studies, and designing medium and long-term research and monitoring programs; iii) applying multi-trophic approaches and promoting research based on the functional traits of the less studied groups of organisms; iv) exploring the role played by the functional traits of less abundant species in ecosystem multifunctionality and the supply of ecosystem services; v) identifying, characterizing, and mapping "multifunctionality providing units", which are defined as spatially-explicit units with high values of functional redundancy and bundles of functional traits that respond to the effects of Global Change, while simultaneously affecting the multifunctionality of ecosystems.

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